Reproductive Strategies in the European Blackbird, *Turdus merula*

Thesis

Reproductive Strategies in the European Blackbird, Turdus merula

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Abstract

In this thesis I explore the reproductive strategies of European blackbirds, *Turdus merula* in Oxford Botanic Garden using detailed observation of marked individuals and tests of genetic paternity. In Chapter Two I establish that the population's breeding ecology is comparable to other studies on the species and identify the importance of nesting cover in both territorial distribution and nesting success. In Chapters Three, Four and Five I demonstrate that both males and females pursue mixed reproductive strategies and engage in extra-pair copulations. Female tactics are covert and, backed up by a review of the literature, I suggest that they are constrained by the costs of attracting sexual harassment from males. I find that males employ counter-strategies of mate guarding and territorial defense and that their tactics vary according to social circumstances. In contrast, I find that females do not use counter-strategies of either close association or repeated copulation, and review of the literature suggests a reconsideration of female mate guarding theory. In Chapter Six I link earlier research into European blackbird breeding ecology with observations from this study to show the influence that availability of dense vegetation for nesting cover has on mate acquisition and subsequent sexual strategies during the breeding season. In addition to the contributions to sexual selection theory described above, this thesis contributes to knowledge of the breeding biology of the European blackbird by adding explanations of the mate acquisition and sexual strategies that give rise to this biology.

Contents

Chapter One: Introduction

Aims of the thesis

The start of this study coincided with a shift in emphasis within behavioural ecology from the study of species-typical behaviour to an emphasis upon individual differences in behavioural patterns, with the recognition that individuals provide the raw material for sexual selection (Creighton & Hosie 1993, Reynolds 1996). For the study of reproductive behaviour, this involved a shift from species-typical mating systems to individual reproductive strategies (Trivers 1972), with the appreciation that the costs and benefits driving the selection of behavioural traits may differ between individuals within the same population (Grafen 1988) and that ecological and social conditions might influence those costs and benefits (Emlen & Oring 1977).

The aims of this thesis were (1) to test current theory on the costs and benefits driving reproductive strategies in birds by (2) exploring in detail the reproductive strategies of individuals within one population, (3) determining how conflicts of interest between individuals are resolved, and (4) exploring the influence of ecological and social conditions on the behavioural traits expressed.

The choice of the European blackbird as the study species followed largely as a matter of convenience, as it is a common species with a well documented natural history (Cramp 1988) whose urban habits would permit close scrutiny of behaviour.

The last decade has seen great advances in the methodology used to tackle research questions in behavioural ecology (Birkhead & Møller 1992, Birkhead & Møller 1998). However, as Davies' (1992) classic studies of the dunnocks *Prunella modularis* in Cambridge Botanical Garden illustrate, the value of detailed observation of behaviour can never be underestimated. Here I use direct observation of marked individuals and a limited DNA fingerprinting study of genetic paternity to test established theory and to generate new insights into explanations of reproductive behaviour.

The limited success of the DNA fingerprinting to permit estimation of rates of genetic paternity of chicks hatched in the course of the study is the major weakness of the thesis. The problem arose partly from the high rate of nest predation (Chapter Two) and from collecting blood samples only in the 1992 and 1993 seasons, resulting in a low number of samples to test; and from limited success in the fingerprinting laboratory reducing still further the number of fingerprints available to score. Despite the combined efforts of the labs at The Open University, the University of Oxford and the University of Leicester only 14 of the 19 chicks sampled from seven broods produced scorable fingerprints.

That said, these data do demonstrate that extra-pair paternity occurs as a consequence of the sexual strategies identified by direct observation and this is sufficient to allow conclusions to be drawn regarding functional explanations of behaviour.

A follow up study in 1996 involved collecting a further 60 samples from 17 broods in urban sites in Cheshire, Greater Manchester and Cumbria. Several sites were used with the agreement of the Home Office to permit a large number of territories to be surveyed in a limited period of time in order to find sufficient nests containing chicks at the appropriate age to be sampled (five to nine days old). It was not possible to use only one site as I was unable to monitor a sufficiently large number of nests throughout the whole breeding season (March to July) in order to collect samples from nests

that succeeded in hatching young when predation rates in urban blackbirds are so high (Chapter Two).

The samples were to be submitted for analysis in the laboratories of Prof. Terry Burke at The University of Leicester, but in 1996 these labs were experiencing as then undiagnosed difficulties with their fingerprinting procedures. The labs in Biological Sciences at *the* Manchester Metropolitan University were having no such problems but were using light probes for the final production of autoradiographs, rather than the radioactive probes used for the original blackbird fingerprints. As the samples could be readily transported after Southern blotting and fixing onto Amersham Hybond-Nfp membranes (see Kirby 1990 for background details), it was agreed to process the samples as far as the membrane stage in Manchester then complete the analysis using the radioactive probes in Leicester. This would ensure that the techniques used were equitable to the original blackbird fingerprints and direct comparisons between the sets of data could be drawn.

Three membranes were sent to Leicester for probing in September 1996 but each produced very poor quality fingerprints. Such problems only become apparent at the end of the long series of procedures used in DNA fingerprinting and as such it is difficult to pin-point exactly where the procedure is failing. However, the extensive experience of the Leicester labs lead them to suggest incomplete enzyme digestion and/or poor transfer of DNA to the membranes was to blame.

On advice from Leicester the analysis was begun again from scratch using what remained of the blood samples. A second set of three membranes were sent to Leicester in December 1996 and revealed some lanes with bands, though these were of poor quality. With the aid of image enhancement software some fingerprints were scorable and Leicester were asked to complete the full diet of long to short exposures to provide fingerprints of different intensity to maximise the number of bands for analysis. However, on re-probing no fingerprints could be obtained, possibly

due to poor membrane quality resulting in the loss of the DNA when the membrane was stripped of the first probe. Without these further exposures it was impossible to gain any reliable data from the fingerprints and with no blood or money left for further attempts I had to reluctantly abandon the study.

Collectively these experiences offer some suggestion for future researchers in how such problems with multilocus fingerprinting of blackbird blood samples may be avoided. None of the fingerprints produced in any of the labs involved were of good quality and all showed evidence of DNA degradation suggesting problems with sample storage and/or with the protocol and the HaeIII digestion enzyme used. Switching storage procedures from freezing in 1X SSC, 10mM EDTA to 100% analar ethanol did not correlate with any improvement and indicated that storage problems alone were not sufficient to explain the problems. DNA extraction protocols were eliminated when salt extraction was replaced with phenol/chloroform extraction with no subsequent improvement. The major culprit emerges as the HaeIII digestion enzyme which does not appear to be particularly suited to blackbird DNA. In all labs slow and/or incomplete DNA digestion was in evidence and required prolonged or repeated procedures to correct it. This exposed the sample DNA to high temperatures for prolonged periods where contamination from environmental enzymes (mainly from airborne bacteria) could lead to random digestion of the DNA and the resultant appearance of degradation. Future attempts at genetic analysis European blackbirds must include trials of alternative digestion enzymes to find one that more readily digests their DNA.

The final problem with the membranes that emerged from the samples processed at *the* Manchester Metropolitan University probably arose from a batch of faulty membranes supplied by Amersham. The source of this problem was finally identified by Leicester as one contributing to

their difficulties in 1996, but was not known at the time my samples were being prepared in Manchester.

Organisation of the thesis

The thesis is organised into seven chapters and two appendices containing published or *in press* manuscripts of material that arose directly from this study or from related work. Each chapter or appendix is presented as a discrete unit complete with its own acknowledgements and reference section and is identified within the text by the running headers at the top of each page.

Following the introductory chapter are five data chapters addressing separate research questions and presented with full discussion of the contribution the data make to the current state of research in the area. At the date of submission, Chapter Five is in print with *Animal Behaviour,* Chapter Four has generated a short communication that is in press with *Ibis* (the manuscript is included in the Appendix), Chapter Three has just been returned from the *Journal of Avian Ecology* with recommendations to submit as a short communication, and Chapter Two in preparation to submit to *British Birds.* Following the data chapters is a short concluding chapter summarising the contribution the thesis makes to knowledge in ornithology and behavioural ecology and outlining suggestions for future research.

Chapter Two provides a review of the breeding ecology of the European blackbird and a comparison of my Oxford Botanic Garden data with those published for this species both in their ancestral woodland and farmland and in other urban sites. The review highlights the importance of nesting cover as the prime ecological feature that underpins the breeding ecology of European blackbirds in both urban and rural habitats. Its role in the thesis is to establish my population as representative of European blackbird populations in general and to provide a platform for drawing

wider conclusions from the sample data collected from the study population.

Chapters Three, Four and Five address the sexual strategies used by European blackbirds, tests current theory on the fitness costs and benefits underlying them and explores how conflicts of interest between the strategies adopted by the two sexes are resolved. Although blackbirds, like the majority of bird species (Lack 1968, Møller 1986) exhibit socially monogamous breeding patterns, their reproductive success is not necessarily limited to reproductive success on their territory (Trivers 1972, Birkhead & Møller 1992).

In Chapter Three I describe the extra-pair copulatory behaviour of both males and females and establish that both sexes are using extra-pair sexual strategies. The tactics used by males correspond well to those described for other similar species and can be readily interpreted in terms of increasing the males' reproductive success. Female tactics are much less overt and, as in may other species, provided less obvious support for either sperm competition or direct material benefit explanations. With reference to the published literature I suggest support for the conclusion arising from my data that conflict between male and female sexual strategies may promote forced copulation tactics by males and that this constrains the overtness of female EPC tactics as a counter-measure. I suggest that this may provide a new consideration for understanding the variation in female extra-pair copulation behaviour seen between different species.

In Chapter Four I address the counter strategies used by males to protect their reproductive interests from the threat posed by the extra-pair strategies of the females. Males adopt mate guarding and territorial defense as their strategy in common with males of other similar species, though they show a relatively novel resolution to the conflict posed between mate guarding by close association and the demands of territorial defense.

In Chapter Five I consider the females' counter strategies to their mates' extra-pair copulations. Despite theoretical predictions to the contrary, female blackbirds do not mate guard by either repeated courtship and copulation or, as newly suggested here, by close association. In a review of the literature to date I point out that there is a split in female mate guarding behaviour between species with socially monogamous breeding patterns and those where polygyny is a threat, and argue that this has implications for the fitness payoffs underlying female strategies.

Chapter Six returns to the ecological and social conditions that influence the costs and benefits underpinning the birds' reproductive strategies. Here I link earlier research into European blackbird breeding ecology with observations from this study to show the influence that availability of dense vegetation for nesting cover has on mate acquisition and subsequent sexual strategies during the breeding season.

In addition to my work on the European blackbird, I include in the appendix a copy of papers jointly authored with Dr Lottie Hosie and arising from an ASAB funded workshop that we organised in 1993. The two day workshop provided the opportunity for PhD students and postgrads to explore the then current status and future of theory of mating systems / individual reproductive strategies. Although the literature has moved on and the chapters included in this thesis reflect the current theoretical and empirical perspectives, these essays provide the background to the theoretical framework that shaped my initial thoughts and investigations into the blackbirds' reproductive strategies at the start of this study.

Natural history of the European blackbird

The natural history of the European blackbird (*Turdus merula*) has been described in detail by D.W. Snow, so only a brief summary will be included here. What follows is based upon information given in Snow (1958a, 1958b) and in a more recent review by Cramp (1988). Further studies providing additional or supporting information are referred to in the text.

Blackbirds are a medium sized (c. 100g) passerine of the thrush family (*Turdidae*). They exhibit little sexual dimorphism in size, but have distinct plumage differences between males and females. The males are uniformly matt black with a bright orange bill and eye ring, and brown legs. The females are variably mottled olive-brown, with a brown bill, eye ring and legs, though the bill may develop limited orange colour during the breeding season. Juveniles of both sexes sport a more speckled, chocolate-brown plumage with a brown bill, eye ring and legs. They moult into adult plumage at the end of their first summer, although juvenile primaries and tail feathers are retained until their second moult (at the end of their second summer) enabling first year birds to be distinguished from older adults.

Blackbirds are common in urban parks and gardens, a habitat that they began to colonise from their original woodland home at the beginning of the last century. As a species they are found throughout Europe, in the more temperate areas of central Asia, and in New Zealand and south east Australia, where they were introduced by European settlers. They are characteristically partial migrants, with territorial birds remaining resident and others (mainly females and juveniles) migrating south or west (in Europe), though residents may make local movements in response to food shortages brought about by cold weather. In the harsher habitats of the more northern latitudes, the whole population migrates south and west for the winter.

Blackbirds feed on a variety of food, particularly insects and invertebrates found on the ground, and on fruit and berries when they are in season. The majority of their food is found on the birds' territories, though areas of open grassland are used communally by migrants and by residents when food is scarce during winter frosts and summer droughts.

The sexes pair in late winter and defend an exclusive territory as an apparently monogamous breeding pair. In Oxford the breeding season begins in late February or early March, depending upon the weather. It may

continue until early July, though in urban sites it tends to end earlier as the summer sun dries out the ground and prey species bury deep into the soil making food scarce (Török & Ludvig 1988). Both sexes usually start breeding when one year old, and up to five nesting attempts may be made in any one season, though this is usually less for first-year birds (Desrochers 1991, 1992). Nesting success is low and three broods at the most will be raised (Snow 1955a, Osbourne & Osbourne 1980, Magrath 1989).

The female alone builds the nest in dense vegetation usually within three metres of the ground. The nest is cup-shaped and made from a weave of dried stalks lined with mud and finished with mosses and/or dried grass. The female lays a clutch of between two and five eggs, with four as the modal clutch size (Snow 1955b, Havlin 1963, Hatchwell et al 1996), though Magrath (1989) reports clutches of three eggs to be slightly more common than four in Cambridge Botanic Garden. Incubation begins as the clutch is completed and lasts for two weeks (Magrath 1989). On hatching the male helps provision the brood (Desrochers 1991) and may briefly brood the young while the female is absent (Gurr 1954), but he does not develop a brood patch. After two weeks in the nest the chicks fledge and remain dependent upon their parents for approximately three further weeks. The chicks are usually split evenly between their parents, so that each feeds only certain fledglings and refuses to feed others. Though the female may start a new clutch within this time, and leave the male to care for all the surviving young (Edwards 1985).

The breeding season is characterised by a dawn and dusk song chorus and intermittent day singing by the males from prominent perches within their territories. At the end of the season the sexes cease to associate. They both remain on the territory during their annual moult in the late summer months, and throughout the winter unless driven to search for food off the territory by severe weather.

The study site

The study was conducted in Oxford Botanic Garden (51°44'N, 1°16'W), southern central England, in 1991-93. The site benefitted from a human-habituated population of blackbirds which could be watched from close range without disturbance, and from the closely manicured horticulture which permitted good visibility throughout most of the garden.

The garden covers a little over six and a half acres and encompasses a seventeenth century walled garden and a newer (twentieth century) extension to the south bounded by dense shrubbery. The site includes mature lawns, cultivated beds, herbaceous borders, alpine and rose gardens, hedges, shrubberies and mature trees, walls covered in climbing plants, fountains and ponds, glass houses and sheds, with footpaths between them all. To the south and east lie open playing fields and meadows and to the north and west private buildings and gardens.

The study population

During the course of the study Oxford Botanic Garden supported between seven and eight breeding territories. One or two additional territories were defended by unpaired males in each year (Chapter Two). Two further breeding territories overlapped the southern end of the garden from the surrounding meadows. However, the dense thorn and evergreen shrubs restricted visibility in this area, and the impossibility of following the rather shy resident birds over the fenced garden boundary made detailed observations of these birds' behaviour impossible.

Adults were trapped under licence from The British Trust for Ornithology (BTO) using either Potter traps (Davis 1981), or a variation where the weight of the bird on the false floor released the hinged door. The majority of adults were caught between January and March, when ground frost limited the availability of natural food and encouraged the birds to enter the traps for a bait of porridge oats. Any remaining unringed birds

were caught on their breeding territories later in the season, after becoming accustomed to entering unset traps for a bait of fruit or cheese. Chicks were ringed on the nest at between six and eight days old, when their legs were sufficiently developed to accept rings, but before they were old enough to prematurely leave the nest after disturbance (Spencer 1984).

Adults were sexed by their plumage colour (Cramp 1988), weighed to the nearest gram using a Pesola spring balance and were assigned to BTO age categories (Spencer 1984). The length of the right wing to the nearest millimetre; and right tarsus and bill length to the nearest tenth of a millimetre, were recorded (Yezerinac et al 1992). The percentage of the outside surface of the bill coloured yellow was estimated by eye and the richest tone matched in natural light to Pantone colour cards (Pantone by Letraset Colour Products Selector, Pantone Inc., USA).

In 1992 and 1993 samples of between 25µl and 180µl of blood were taken from adults and chicks by venipuncture of the right brachial artery, under Home Office Licence (personal licence No. PIL 30/3103, under project licence No. PPL 30/00715 held by Professor C. Perrins of the University of Oxford, and No. PPL 50/1345 held by the author).

The birds were marked with coloured leg rings for individual identification. Adults were given five coloured plastic rings and a numbered aluminium BTO ring (Spencer 1984) - three rings on each leg. The sex of the bird and the colour order of its leg rings provided a unique combination for each bird. Chicks were marked with individual combinations of one or two coloured rings, and a numbered aluminium BTO ring. Any that were recaptured and sexed in adult plumage were re-marked with an adult ring combination.

Coloured leg rings are widely used in bird studies. A large range of colours are available and the number of unique combinations would seem only to be limited by the visibility of the colours in the study bird's habitat. However, studies have shown that the colour of a ring can have profound

effects on a bird's behaviour and the behaviour of others towards it, with significant consequences upon reproductive behaviour and/or success (Burley 1981, 1985, 1986a, 1986b, Burley et al 1982, Brodsky 1988, Hagan & Reed 1988, Metz & Weatherhead 1991, Holder & Montgomerie 1993, Johnson et al 1993). In order to minimise these problems, the marked birds all carried one each of light green, red, light blue, pink and striped black/white coloured rings, and an aluminium BTO ring. The colours orange and yellow, which may have had an enhancing effect on the birds' possible secondary sexual characteristics (Brodsky 1988, Metz & Weatherhead 1991), were avoided.

Within each sex the order of the coloured rings and the position of the BTO ring amongst them identified each bird. The scheme was simplified by maintaining the order of colours until a conspicuous change was dictated by the exhausting of all possibilities. Identification then merely required the determination of the position of the BTO ring and an indication of the order of the coloured rings, from which the remainder could be deduced.

Six rings were used, which provided 576 unique combinations. This large number meant that birds could be ringed in the winter months, when the risk of losing ring combinations to migrants is high, without the problem of running out of combinations.

Despite its relative complexity, no problems were encountered in using this marking scheme. The birds readily adapted to their markings, and on their recapture no complications were found to be associated with the wearing of so many rings. The simplified identification procedure, the birds' tameness, and the open and neatly manicured habitat, ensured that all birds whose legs could be seen were readily identified using either Optolyth 8X40 Alpin binoculars or an Opticron X20-60 AA64-60S spotting scope.

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Chapter Two: The importance of nesting cover in the breeding ecology of the European blackbird

Studies of the breeding biology and related ecology of European blackbirds, Turdus merula *are widespread and encompass the full range of habitats. Together they provide a rich data-base against which to compare individual studies and to draw widespread conclusions. This paper reports on the breeding ecology of a small study on a colour-ringed urban population occupying a habitat undergoing ecological change. Comparisons with other studies support the findings that breeding territory distribution was affected by changes to vegetation cover, that low fledging success was largely due to predation, and that predation risk, and so reproductive success, was related to the availability of nesting cover on the breeding territory. Together the data support the conclusion that vegetation cover underpins territorial distribution and fledgling success, highlighting the importance of nesting cover to the breeding ecology of the European blackbird.*

Introduction

This paper reports upon the breeding biology of the European blackbird *Turdus merula* in Oxford Botanic garden in the early 1990's and explores ecological explanations for variation in nesting success in this and in other populations.

The European blackbird is a medium sized, socially monogamous territorial passerine common to both urban and rural habitats throughout Europe, much of central Asia and as an introduced species in New Zealand and southeast Australia (Cramp 1988). Open nests are built generally in dense shrubbery with a median clutch size of four eggs and up to six nesting attempts per pair over a prolonged breeding season ranging from late January to June in southern UK (Cramp 1988).

The breeding biology of the Oxford Botanic Garden (OBG) blackbirds has been recorded in detail during two other studies over the course of the second half of the twentieth century (Edwards 1983, Snow 1958a). Other detailed studies in similar urban habitats (Magrath 1989, Desrochers 1991) allow comparisons to establish the degree to which the OBG population is representative of urban populations in general. A smaller number of studies of rural populations and summaries of data from the British Trust for Ornithology (BTO) nest record scheme provide a wider picture of the birds' breeding biology in their ancestral rural habitat and across all habitats in general (see references in Table 3).

During the course of this study restoration work to the ancient garden walls and changes in the horticultural focus of the OBG resulted in some quite radical changes to the vegetation structure of the study site. This provided the opportunity to observe the effect of habitat change on the birds' breeding ecology and to add a manipulative slant to the largely observational studies reported in the literature.

Study Site and Methods

The study was conducted on a colour-ringed population in Oxford Botanic Garden (51°44'N, 1°16'W), southern central England in 1991-93 as part of a wider study of the birds' reproductive behaviour. The OBG covers a little over six and a half acres and encompasses a seventeenth century walled garden and a newer (twentieth century) extension to the south bounded by dense shrubbery (Figure 1). To the south and east are open playing fields and meadows and to the north and west are private buildings and gardens.

I observed the outcome of nesting attempts where clutches were initiated by resident pairs of blackbirds. Nests were found by following females collecting nesting material and by occasional systematic searches of territories when a nesting attempt was suspected from the birds' behaviour. Nests were checked when the birds were elsewhere to determine the date of clutch initiation and the final clutch size. The outcome of nesting attempts were defined as abandoned if the nest was begun or built but no eggs were laid; predated if a clutch was initiated but its contents disappeared and the birds deserted it; deserted if a clutch was initiated but then deserted by the birds leaving the contents behind; and successful if chicks were fledged.

I deduced breeding territory outlines by marking the position of any boundary disputes with neighbours and the positions of resident birds on a map of the site at one minute intervals during regular 20 minute focal watches of the birds' behaviour over the course of the breeding season. Territory boundaries were readily drawn by combining these positions over many focal watches.

The start of the study coincided with the beginning of a major overhaul of the garden including restoration of the garden walls and redefinition of many of the species beds. Many well-established shrubs were pruned or removed, greatly reducing the available cover. The proportion of lawns, paths and open beds did not change, though the amount of exposed soil increased.

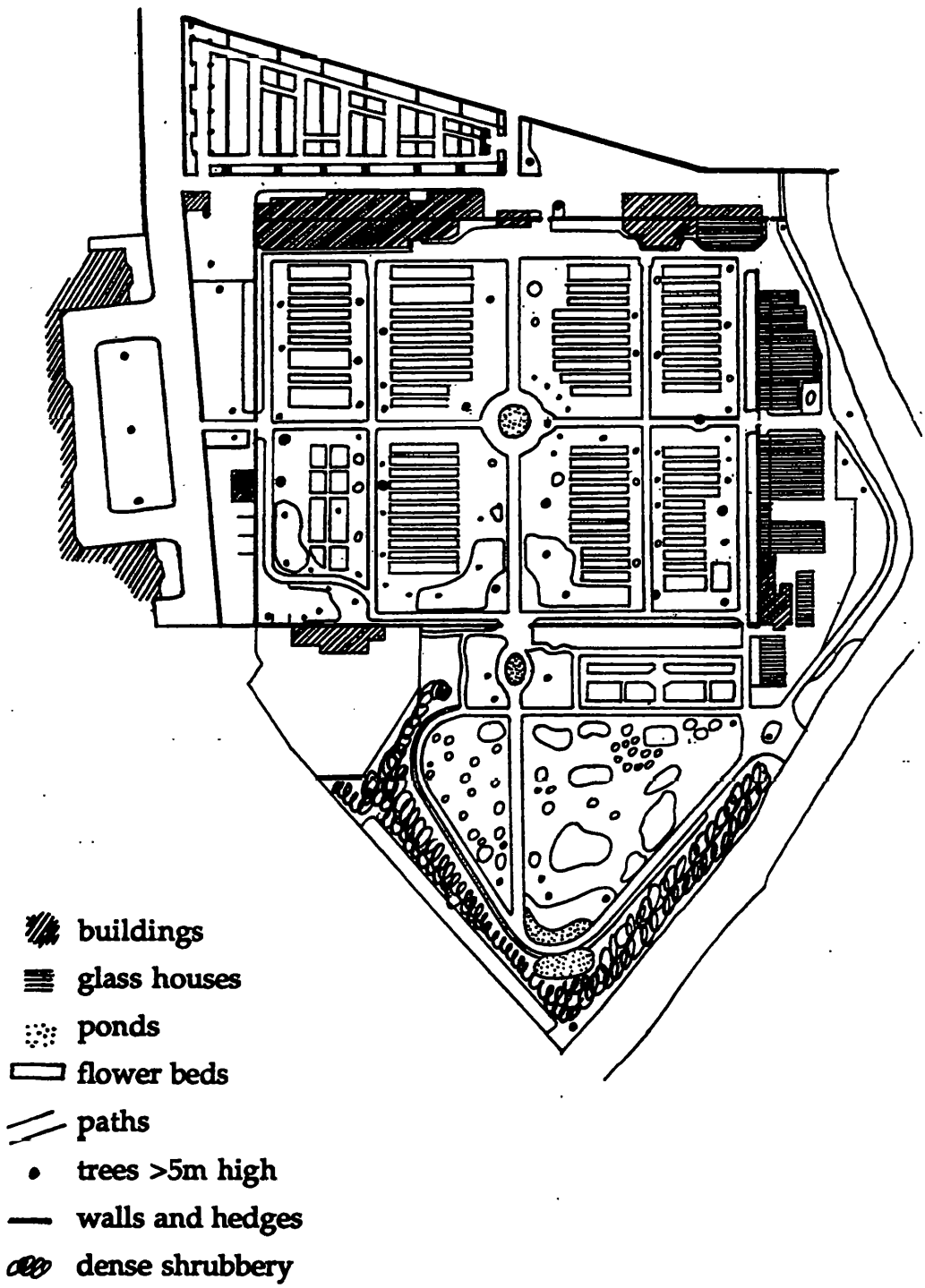


Figure 1. Map of the study area in and around Oxford Botanic Garden showing the major topographical features

Prior to the start of the study the east wall was cleared of shrubs and climbers to below the lip of the coping stones and the remaining vegetation severely pruned. Throughout 1991 the south wall was cleared on both sides for masonry work and redesign of the borders which lasted until the end of the 1992 season. What had been a thick layer of dense vegetation on both sides of the wall was reduced to occasional patches of closely pruned climbing ivy with young vegetation or herbaceous borders in the beds below. The outer side of the west wall was stripped of most of its shrubs and climbers climbers in the winter of 1991/92 and on the garden side the shrubs and climbers were pruned back to the lip of the coping stones. In the winter of 1992/93 the garden side was largely cleared much reducing the vegetation cover along this side of the garden. The walled garden side of the north wall was completely cleared of climbers and shrubs in the winter of 1991/92, though the climbing vegetation and shrub border clothing the much of the outer side of the buildings making up this boundary were left intact. The rose garden to the north of the OBG, the service areas to the east, and the new garden to the south were relatively little changed, with only one large thicket of dense shrubbery being removed from the east side of the new garden in the winter of 1991/92.

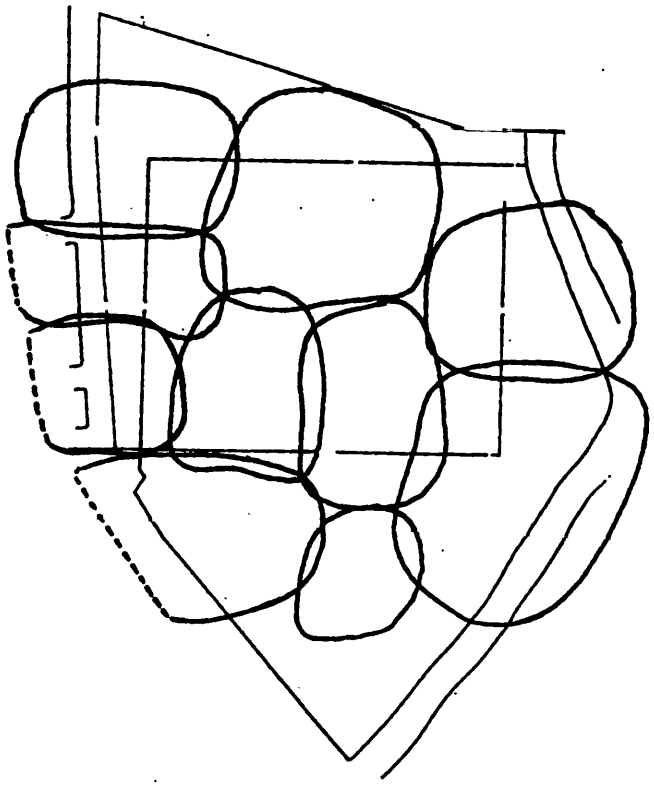
Results and Comparison with Other Studies

Breeding territories

During the course of the study seven or eight breeding territories and one or two territories defended by unpaired males could be closely monitored per year (Figure 2). All breeding territories were occupied by socially monogamous pairs.

One incidence of divorce was observed. The female left a surviving male with whom she had successfully raised a brood the previous year, to take over the territory of an old female who died in late January 1992. Her

a) early 1991



b) late 1991

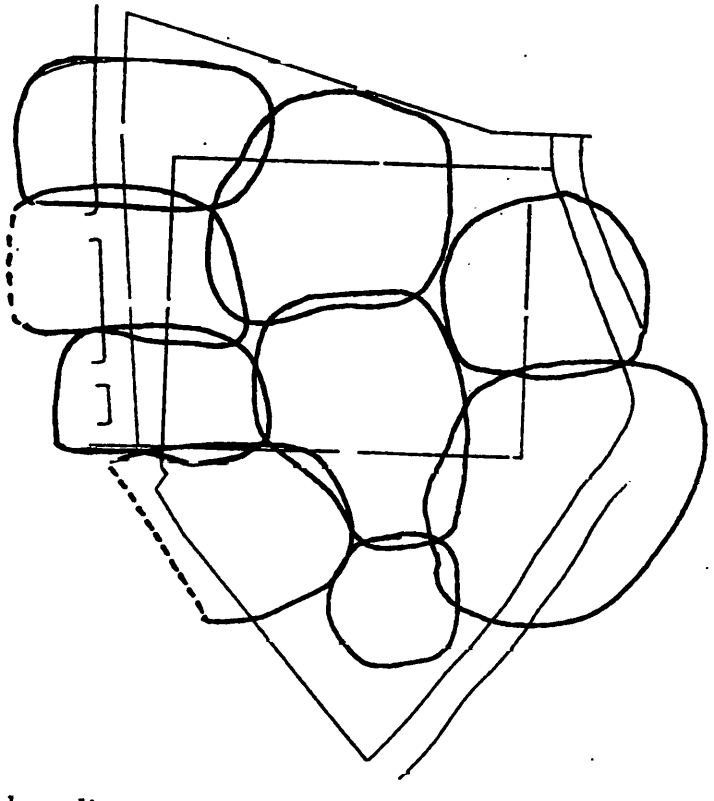
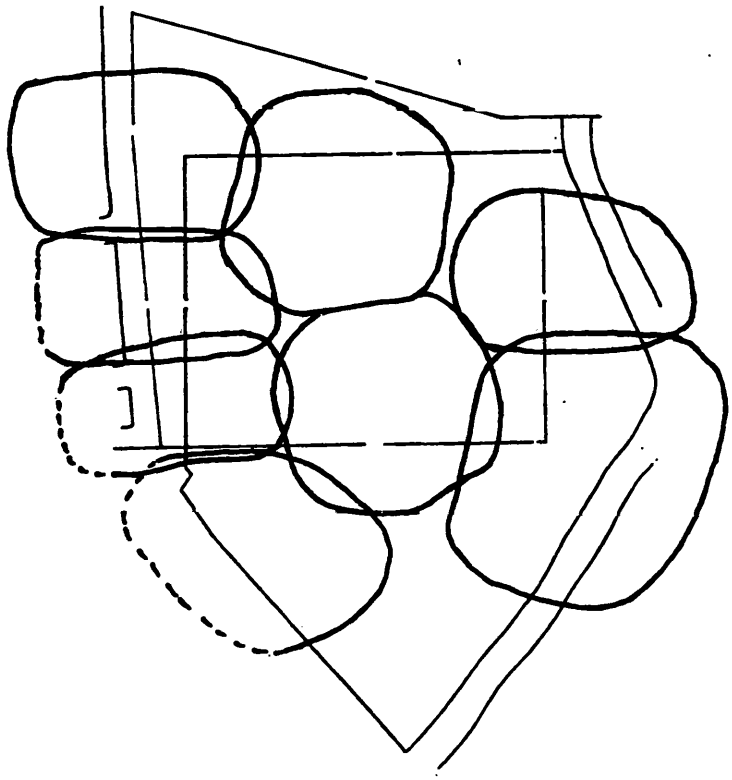


Figure 2. Outlines of breeding territories the 1991 breeding season.

c) 1992



d) 1993

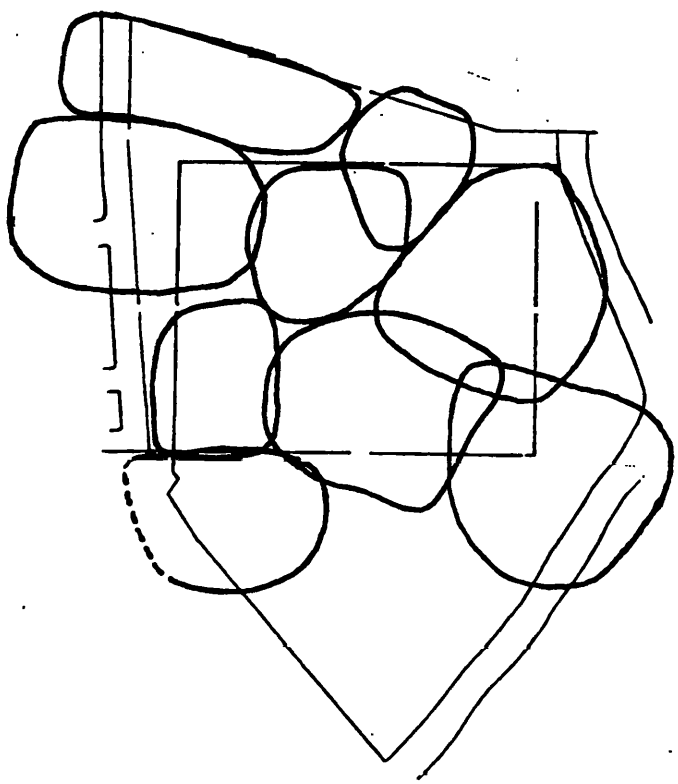


Figure 2 cont. Outlines of breeding territories the 1992 and 1993 breeding seasons.

move followed the loss of vegetation cover due to restoration work to the garden. Her new territory to the south of the south Wall was relatively untouched and included dense shrubbery and climbing plants. Desrochers & Magrath (1993a, 1996) have shown that blackbirds break pair bonds more readily in poor breeding sites than in good ones, and supports the suggestion that this female was leaving an impoverished breeding site for one of superior quality.

The territories of the unpaired males were either along the east wall of the garden where the shrubbery and climbing vegetation had been stripped prior to the start of the study or in the centre of the new garden where the habitat was mainly lawns and rockery.

Changes to the distribution of breeding territories occurred from year to year (Figure 2). At the start of the restoration work in the 1991 breeding season, one territory on the south wall was abandoned after the climbing plants and shrubs were removed from that part of the wall. The vacancy was absorbed by the expansion of the two neighbouring territories. In the winter of 1992 the west wall was cleared and again a territory was lost in this area for the 1993 season and the vacancy was absorbed by the expansion of the two neighbouring territories. However, this shift south by the northern-most territory on the west wall and the reduced territory of the north wall male with a damaged foot, created a vacancy to the north of the walled garden and a new breeding territory was established.

These changes in the pattern of breeding territories is in direct contrast with earlier studies in the OBG where the arrangement of breeding territories remained largely constant (Snow 1958a, Edwards 1983) and where Edwards was able to identify the same territorial patterns in 1979-81 as Snow described in 1953-56 (Edwards 1983). However, Edwards (1983) does describes two changes and in both cases, as here, attributes the cause of the change the removal of dense shrubbery or climbing plants.

Nesting attempts

I observed a total of 55 nesting attempts by 22 pairs where a clutch was initiated. There were up to four breeding attempts per pair in breeding seasons spanning March to June (Figure 3). This is comparable to other studies of urban populations in southern UK (Snow 1958a, 1958b, Myres 1955, Batten 1973, Desrochers & Magrath 1993b).

Although not statistically significant, the data indicate variation in the success of first to fourth nesting attempts (Table 1). Snow's (1966) analysis of the UK nest records identifies nesting success by calendar month and finds a decrease in success from March to April nests followed by an increase in May and June nests. In this study the successful nests were either early nests or later nests, corresponding to Snow's findings, though the late start to the 1992 season put the early successful nests into early April (Figure 3).

Nesting success

Fledging success was low in every year (Table 1) with an average fledging success of 27.3 % of nests where a clutch was initiated. This is lower than reported in the OGB earlier in the century and in nearly all of the other studies on urban habitats, though rural habitats generally have a lower success (Table 3).

In 1991 and 1993 the majority of nests were lost to predation, and as Snow (1958a) found, usually at the egg laying or incubation stage (Table 2). Predators included magpies (*Pica pica*), jays (*Garrulus glandarius*), crows (*Corvus corone*), and occasionally some sort of mustelinae which was never positively identified. Contrary to the findings of other studies (Osbourne & Osbourne 1980, Magrath 1989), the resident grey squirrels (*Sciurus carolinensis*) were never observed to raid nests, and their presence was ignored by the birds, who greeted all other known predators with alarm.

Table 1. Summary of nesting success of nests where clutches were initiated. Over-all fledging success over all three seasons was 27.3%

		Nesting success by attempt				
Year	Pairs	1st	2nd	3rd	4th	Total
1991	8	3/8 (38%)	1/6 (17%)	0/6	0/1	4/21 (19%)
1992	7	2/7 (29%)	3/7 (43%)	1/4 (25%)	0/1	6/19 (32%)
1993	7	2/7 (29%)	2/5 (40%)	1/2 (50%)	0/1	5/15 (33%)
Total[1]	22	7/22	6/18	2/12	0/3	15/55

1. G-test for goodness of fit with William's correction after pooling 3rd and 4th attempts, G_2=1.72, P>0.05.

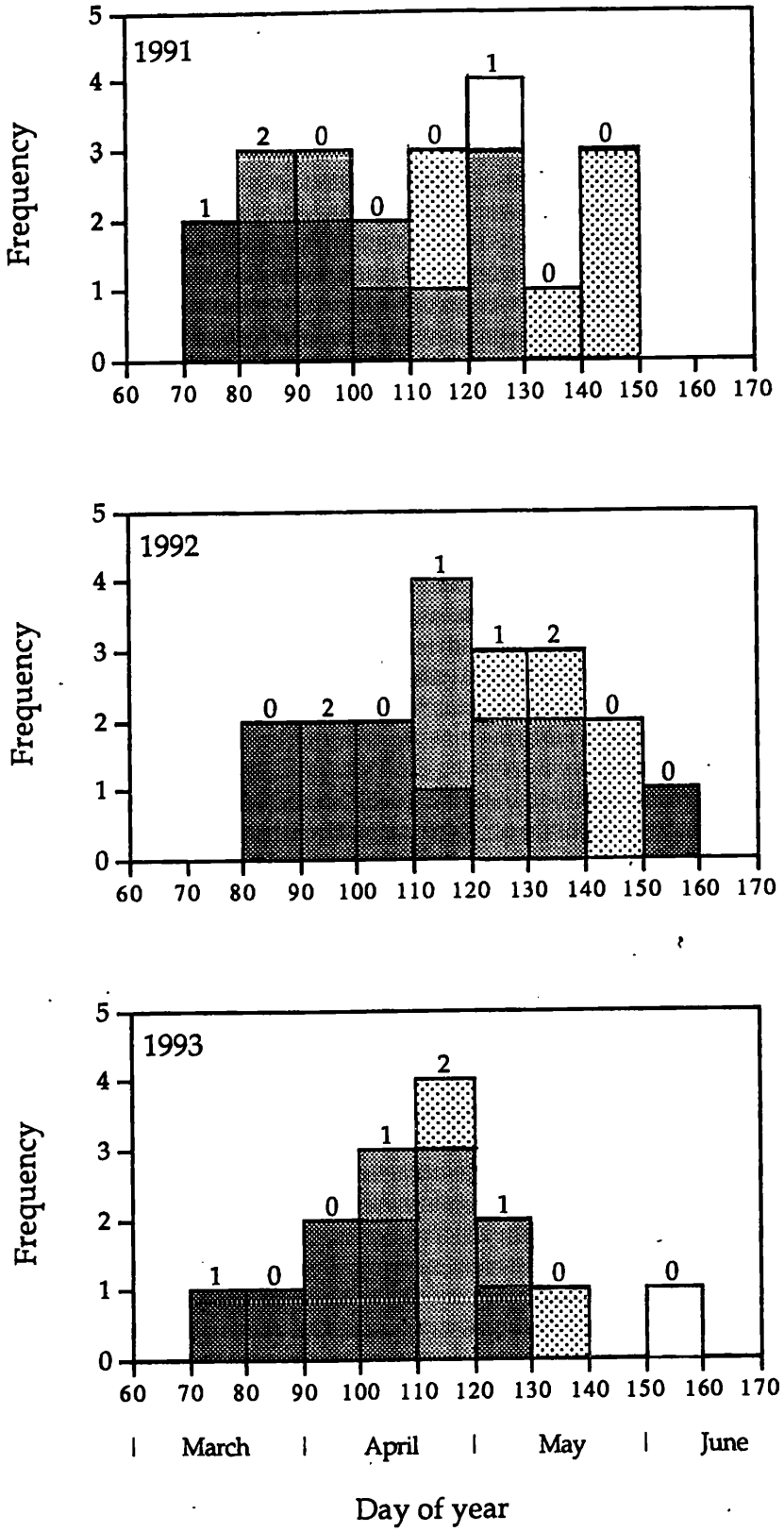


Figure 3. Frequency plots of clutch initiation dates in ten day blocks. First to fourth clutches are indicated by shading gradation from dark to clear. Values above indicate the number of successful nests per block.

Table 2. Summary of stages and causes of failure of nests where clutches were initiated

	Nests		Stage of nest failure (% failed nests)			Cause of loss	
Year	Total	Failed	Lay	Inc.	Chick	Predated	Deserted
1991	21	18 (86%)	4 (22%)	13 (72%)	1 (6%)	12 (67%)	6 (33%)
1992	19	13 (68%)	7 (54%)	6 (46%)	0	3 (23%)	10 (77%)
1993	15	10 (67%)	5 (50%)	5 (50%)	1 (10%)[1]	7 (70%)[1]	4 (40%)

1. partial predation, with three chicks taken and one surviving to fledge.

Table 3. Comparison of nesting success and causes of failure with other studies of European blackbirds

Site	Nesting sucess	Cause of nest failure		Source
		Predation	Desertion	
Oxford Botanic garden, UK				
1991-93	26%	68%	36%	This study
1979-81	37%	69%	30%	Edwards 1983
1953-56	50%	74%	26%	Snow 1958a
Wytham woods and fields, Oxford, UK, 1991-3				
1991-93	19%	92%	6%	Hatchwell et al 1996
1954-56	14%	-	-	Snow 1958
Cambridge Botanical Garden, UK, 1985-1990	37%	73%	27%	Desrochers 1991
Budapest, Hungary, 1986-89	43%	-	-	Ludvig et al 1995
Greater Manchester, UK, 1988-90	13%	97%	3%	Groom 1993

Australian nest records scheme 1963/4 - 1986/7				
urban	45%	-	-	Kentish et al 1995
rural	34%	-	-	Kentish et al 1995
overall	42%	66%	34%	Kentish et al 1995
Exeter University Campus, UK, 1977	33%	71%	29%	Osbourne & Osbourne 1980
UK Nest records scheme				
1951-65	33%	78%	22%	Snow 1966
1948-53	41%	69%	30%	Snow 1955
Czechoslovakia nest records scheme, 1948-61				
urban	69%	-	-	Havlin 1963
rural	63%	-	-	Havlin 1963
Rural Scotland 1948-51	62%	-	-	Venables & Venables 1952

In 1992 the largest cause of nest failure was desertion during egg laying or incubation, caused largely by disturbance arising out of the restoration and redesign work on the garden. These data have therefore been excluded from the calculation of overall percentages of predation and desertion, leaving figures that are comparable to other studies where the cause of nest failure has been documented (Table 3).

Variation in nesting success

There was a large variation between pairs in the number of young fledged (range 0-6, mean 2.8 fledglings per pair) with ten pairs across three seasons failing to fledge any young at all. Edwards (1983) reports a similar variation from the site in 1979-81 (range 0-7, mean 2.8 fledglings per pair), though Snow in 1963-56 (1958a) finds a greater variation (range 0-13, mean 4.1 fledglings per territory) in keeping with the higher nesting success in the population at that time (Table 3).

Discussion

This study found that the pattern of breeding territories was affected by the changes to the vegetation structure of the garden and that loss of vegetation cover promoted both loss of territories and territorial movements by individuals. The conclusion that vegetation cover underpins territorial patterns is supported from other studies where territorial density has been found to correlate with vegetation cover (Havlin 1963a, Karlson & Källender 1977, Hatchwell et al 1996a).

The fledging success of nesting attempts provided some indication of variation over successive attempts. Comparisons with data from the UK nest records scheme suggests a seasonal effect with greater success in early and late nests. Snow (1966) attributes this variation to the low predation of the relatively few nests built by older, more experienced birds early in the season followed by a drop in success as the number of nests increases and

the inexperience of young birds alerts predators to the availability of eggs. In May and June increasing vegetation cover provides better protection for all nests and the predation rate reduces.

As found in other studies of blackbirds, over-all nesting success was low with losses attributed to predation and desertion. Several studies have found a correlation between predation loss and the vegetation cover and/or degree of exposure of nests (Havlin 1963b, Osbourne & Osbourne 1980, Landmann 1991, Hatchwell et al 1996b, but see Kentish et al 1995), again indicating the importance of nesting cover to reproductive success.

There was a large variation in seasonal fledging success between pairs on different territories in this and other studies. Edwards (1983) found a correlation between success and available nesting cover on individual territories, but not between success and available food supplies. Desrochers & Magrath (1993b) add the influence of age to this variation, with an improvement in success with female maturity independent of nesting cover.

In summary, findings from this study and comparable research in other populations of European blackbirds indicate that breeding territory distribution was affected by changes to vegetation cover, that low fledging success was largely due to predation and that predation risk, and so reproductive success, was related to the availability of nesting cover on the breeding territory. Together the data support the conclusion that vegetation cover underpins territorial distribution and fledgling success, and they highlight the importance of nesting cover to the breeding ecology of the European blackbird.

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Chapter Three: Extra-pair reproductive strategies in the European blackbird

Whilst many studies have used estimates of extra-pair paternity to infer the cost-benefit trade-off of the social, ecological and life-history factors that influence extra-pair strategies, relatively few have focused upon the factors that constrain the choice of tactics used. Observation of extra-pair copulation (EPC) tactics and DNA fingerprinting analyses of paternity revealed mixed reproductive strategies in urban European blackbirds, Turdus merula. *Males sought EPCs by opportunistic intrusions onto their neighbours' territories. Males intruding alone attempted to court the resident female, but when several males intruded together they chased her, attempting to force her to the ground and force copulations (FEPC). Females ignored or flew away from the majority of singularly intruding males and only occasionally responded with covert solicitation leading to copulation. They vigorously resisted all FEPC attempts. Females were never observed to solicit extra-pair males or to leave their territory to visit neighbouring males. A review of the literature on female EPC tactics supports the conclusion that the potential loss of male parental care does not constrain females' EPC tactics, but that the risk of stress and injury from FEPC attempts by neighbouring males attracted by overt sexual behaviour does. There was no behavioural or genetic evidence of intra-specific brood parasitism in this population.*

Introduction

Extra-pair reproductive strategies are reported in a wide range of avian species, including those in socially monogamous reproductive patterns (Birkhead & Møller 1992, Birkhead 1998). Most frequently these strategies involve extra-pair copulations (EPCs) leading to extra-pair paternity (EPP). Less frequently females may employ the tactic of laying additional eggs, that may or may not be fertilised by the resident male, in other female's nests to be raised at the expense of another pair's parental care (intra-specific brood parasitism) (Yom-Tov 1980, Rohwer & Freeman 1989, Petrie & Møller 1991). However this strategy depends upon a high degree of egg laying synchrony (Petrie & Møller 1991) and in species with asynchronous breeding cycles extra-pair copulations are the predominant strategy (Birkhead & Møller 1992).

Many studies using DNA fingerprinting analyses have found morphological, behavioural or life history correlates of extra-pair paternity success (see Møller & Ninni 1998 for a recent review) and a small but increasing body of evidence demonstrates the fitness benefits to the offspring of extra-pair paternity (Mulder et al 1994, Hasselquist et al 1996, Kempenaers et al 1997, Sheldon et al 1997). From this it is inferred that females use EPC strategies and exercise choice over EPC mates. However, detail of the behavioural tactics used to achieve these EPCs and the cost-benefit trade-off underlying the choice of tactics are rather less well documented (Stutchbury 1998).

The potential benefits of EPCs to males are readily understood in terms of increased reproductive success from extra-pair offspring without the cost of parenting (Trivers 1972). The benefits to females are rather less obvious since copulating with extra-pair males does not typically increase female's clutch size (Stacey 1982). However, females of many species have been found to actively pursue extra-pair copulations (eg Smith 1988,

Kempenaers et al 1992, Wagner 1992a, Sheldon 1994a, Gray 1996, Hoi 1997, Neudorf et al 1997).

Females may benefit from EPCs by increasing the genetic quality or diversity of their off-spring (Smith 1988, Kempenaers et al 1992, Otter et al 1994, Hasselquist et al 1996, Kempenaers et al 1997); by insuring against low fertility of their mate (Wetton & Parkin 1991, Wagner 1991a, Sheldon 1994b, Gray 1997a); by securing additional non-genetic benefits from extra-pair mates (Davies 1985, Gray 1997b); and by strengthening extra-pair bonds as an investment for future matings (Colwell & Oring 1989, Wagner 1991b, Heg et al 1993, Cézilly & Nager 1995).

However, engaging in EPCs also pose potential costs to females from aggression by EPC males or retaliation from their mate (eg McKinney et al 1983, Frederick 1987a); from a reduction in parental care by her pair male (Whittingham et al 1992, Westneat & Sherman 1993); from an increased risk of contracting sexually transmitted diseases (Sheldon 1993, but see Lombardo et al 1999); and in low density populations there may be the additional cost of finding an EPC mate (Petrie & Kempenaers 1998).

Males engaging in EPCs also face costs, including the risk of injury from the extra-pair female's mate (eg Birkhead 1979, Frederick 1987a, Wagner 1992b); the risk of contracting sexually transmitted diseases (Sheldon 1993, but see Lombardo et al 1999) and the energetic costs of finding and courting EPC mates (eg Kempenaers et al 1992, Mulder & Magrath 1994). In addition they may risk loss of paternity with their pair-female due to temporary low fertility arising from sperm depletion (Birkhead 1991, Gray 1997a) and due to neglecting mate guarding at home whilst in pursuit of EPCs (eg Hasselquist & Bench 1991, Dickinson 1997). Extra-pair copulations may also weaken the bond with his pair-mate (Birkhead et al 1985, Wagner 1991a).

In socially monogamous males, the benefits of increased reproductive success from EPCs is likely to outweigh the costs (Yezerinac et al 1995) and

males are expected to actively seek EPCs, usually by intruding onto other territories to court the resident female or attempt to force copulations upon her (Birkhead & Møller 1992). In females the optimal outcome of the costs and benefits of EPCs is likely to be more variable (Petrie & Kempenaers 1998, Johnson & Burley 1998). If EPCs are forced, it seems likely that females do not benefit, though this is complicated by the observations that females in some species seem to use resistance as a tactic to measure male quality (eg Wagner 1991b). Where females use tactics to exert some control over EPCs, then females would seem to benefit. Though again, this may be complicated by the observation that females may accept EPCs when the costs of rejection are very high. For example, incubating females may accept EPCs when resistance could result in damage to their eggs (Røskaft 1983, Frederick 1987a).

Female extra-pair copulation tactics fall into three categories (Stutchbury & Neudorf 1998): (1) females may avoid fertilisation from undesirable males by the rejection of EPC advances (eg Møller 1988, Wagner 1991b, Burley et al 1994, Mills 1994), though this offers no control over which males attempt EPCs; (2) they may encourage advances from EPC males to expand upon their choice by overt solicitation or advertisement of fertility (eg Montgomerie & Thornhill 1989, Sheldon 1994b, Hoi 1997); and (3) females may actively seek EPCs by visiting chosen males on their territories (eg Smith 1988, Kempenaers et al 1992, Smiseth & Amundsen 1995, Gray 1996, Neudorf et al 1997), which has the added advantage of avoiding interference from their social mate.

Such behavioural selectivity by females for extra-pair copulation mates is in conflict with the males' less discriminating strategy, where an EPC with any female that may lead to extra-pair paternity is of value. Where males can gain the upper hand, this conflict may result in males forcing copulations upon unwilling females (Birkhead & Møller 1992).

In this paper I describe the extra-pair copulation tactics of an urban population of European blackbirds, *Turdus merula*, and their incidence of extra-pair paternity. I examine the costs and benefits of the tactics revealed and conclude with a comparative review of the literature on female EPC tactics and the incidence of FEPCs.

The European blackbird is a socially monogamous territorial passerine. Pairs defend exclusive territories throughout the breeding season with up to four nesting attempts (Snow 1958a, 1958b). Open nests are built in shrubbery and predation rates are high (50-95% Chapter Two). Males guard their mates during their fertile period and vigorously defend their territory boundaries against incursions from their neighbours and intrusions from other males (Chapter Four). Females do not appear to mate guard their mates (Creighton 2000 - Chapter Five).

Methods

Behavioural observations

I studied a colour ringed population of European blackbirds in Oxford Botanic Garden, UK (51°44'N,1°16'W), from 1991 to 1993 as part of a wider study on the birds' reproductive behaviour. I followed 16 male-female pairings, involving 12 males and 13 females. Each year between January and June I caught individuals in Potter traps (Davis 1981). The birds were aged and sexed by plumage characteristics (Snow 1958b). I measured their wing and tarsus length (Spencer 1984; Yezerinac et al. 1992) and estimated by eye the percentage of the bill coloured yellow-orange and, from March 1991, the richest tone of this colour as matched in daylight to Pantone colour cards (Pantone by Letraset Colour Products Selector, Pantone Inc., USA, 1989).

I calculated an index of body size for each bird in each year from principal components analysis of wing and tarsus length. The PC1 scores derived explained 72.0% of the variance with character loadings of 0.85 for both measures. T score transformation (Howell 1997) converted these into

positive integers. I calculated an index of bill colour for each individual in each year using derivatives from the seasonal maximum of percentage of the bill coloured orange/yellow, multiplied by the rank of the colour from yellow to orange made by three naive observers from the 16 Pantone colour codes used in the study.

I observed nesting attempts from nest-building to fledging or until the attempt was lost, with the majority of observations concentrated on the days leading up to and including egg-laying. I collected data at all times during daylight hours, with a peak between 0600 and 1100 hours BST. Observations began when I located a focal pair on their territory and lasted 20 min or until the birds were lost from view for 2 consecutive min. Mean watch duration was 18.3 min, with an average of 5.5 watches per attempt and a total observation time of 67.41 h. I watched the birds from the periphery of their territory with no attempt at concealment, since they were habituated to human presence. The order in which the pairs were watched was random on each field day.

I recorded (1) observed copulation behaviour; (2) male courtship behaviour and the target female's response; (3) territorial intrusions, the reactions of the resident birds, and the sex and where possible identity of the intruding bird; (4) moves initiated by the female of a distance greater than 5m or out of perceived visual contact with the male, excluding moves to the nest. Detailed descriptions of courtship and copulation behaviour are provided in Snow (1958b).

I collected data over 41 nesting attempts where the date of clutch initiation was known (37% first attempts, 39% second, 22% third and 2% fourth attempts). The date of clutch initiation and the final clutch size were determined from nest checks. Two nests were not found until after egg laying, and I estimated their date of clutch initiation from the day the chicks hatched, 13 days after the last egg was laid (Snow 1958b). Fledgling success was low (27% of nests in which a clutch was initiated fledged young, Chapter

Two) and 38% of pairs did not succeed in rearing young. Across all three seasons, only three further nesting attempts were made after a brood fledged successfully.

Statistical methods

The presumed fertile period started on day -7 and ended on the morning the penultimate egg was laid (Birkhead & Møller 1992, Birkhead 1998). Most of data were not normally distributed and not readily amenable to transformation, so I used non-parametric statistical treatments unless otherwise stated. Rates of behaviour were derived from the duration of the watch and when combining data from several watches, I weighted averages by watch duration.

Following Davies & Hatchwell (1992; Hatchwell & Davies 1992), I assume that the data for each breeding attempt are independent. Although six pairs contributed only one attempt, 10 contributed between two and seven (median 2.4) and may have introduced error from repeated sampling. However I have shown elsewhere that the variation in male and female pair-association behaviour between different pairs was no greater than that within individual pairs over repeated attempts, indicating that the data were not biased by these repeated measures (Chapter Four; Creighton 2000 - Chapter Five). Similarly, by including some individuals more than once when paired to different partners in different years, the data may be biased from repeated measures of the same individual. However conservative analyses that included each individual only once, show the same patterns of pair-association behaviour as the full data set and indicate that the data were not biased by repeated measures of the same individual in different pairings (Chapter Four; Creighton 2000 - Chapter Five).

DNA fingerprinting

In 1992 and 1993 samples of between 25–180µl of blood were taken from adults and chicks by brachial venipuncture and stored at -20°C in 500ml of 1X SSC 10mM EDTA. The standard multi-locus finger-printing

protocol described by Burke & Bruford (1987) and Bruford et al (1992) was used in the Department of Zoology at the University of Leicester, UK, and the Department of Zoology at the University of Oxford, UK. DNA was digested with *Hae*III, separated on 28cm of 1% agarose gel, transferred to Hybond-Nfp membranes by Southern blotting and hybridised with Jefferys 33.15 probe (Jefferys et al 1985a).

To avoid errors due to uneven running of the DNA on the gel, comparisons of fingerprints across no more than three lanes were made. Bands were scored as different if their centres lay more than 0.5mm apart or if they differed markedly in intensity, when taking over-all intensity into account.

When fingerprints from both sets of putative parents were available, parentage was determined by exclusion analysis. Random mutations are expected to occur at a rate of 1 in every 100-300 bands (0.33- 1%) (Jeffreys et al 1985a, 1985b, Burke & Bruford 1987, Westneat 1990), so unshared bands in offspring at a greater rate were taken to indicate that the parentage of the chick was not correctly assigned.

Band-sharing coefficients (S) were calculated for chicks and putative mothers, chicks and putative fathers and between chicks in the same brood, using the formula $S = 2N_{ab} / (N_a+N_b)$ (Wetton et al 1987), where N_a and N_b are the number of bands for individuals 'a' and 'b' and N_{ab} is the number of bands shared by both. As a measure of the level of band-sharing between first-order relatives, coefficients were calculated between the individuals known from the exclusion analysis to be related. As a background measure of band-sharing, coefficients were determined between presumably unrelated adults run on adjacent lanes.

To exclude parentage in families where the fingerprints of one or both parents were not available, one-tailed 95% confidence limits were calculated from arcsine-transformed band-sharing coefficients of known first-order relatives and of presumed unrelated individuals. Chick-parent or

between-sibling coefficients that fell below the lower 95% confidence limit of first-order relatives were taken to indicate extra-pair parentage.

Results

Copulations and courtships

Blackbird copulations are very brief and infrequent, usually occur at first light and often in dense vegetation (Snow 1958b, pers obs). They are therefore difficult to observe and only seven were observed where both birds could be identified by their leg rings (Table 1). Six occurred during the breeding season and five of these involved extra-pair males. Three of these five EPCs were unforced and took place on the female's territory when the resident male was absent. The other two were FEPCs during the pursuit of the female by a group of extra-pair males (group pursuit). Apart from the one unforced EPC during pair formation, all copulations took place during the females' presumed fertile period.

Group pursuits occurred when three of more males invaded the female's territory at the same time and overwhelmed the pair male's territorial defense behaviour. They chased the female over a short distance uttering highly excited chattering calls whilst attempting to mount and force a copulation. On all occasions the female fled uttering high pitched alarm rattles, but was usually prevented from flight by the males' attempts to mount. If she did become airborne, the chase sometimes continued for a few seconds through the air with the males seemingly trying to force her to the ground. During all this, the resident male attacked the pursuing males, apparently trying to prevent copulations taking place. The one in-pair copulation that was observed occurred immediately after a FEPC during one of these pursuits, and it did not appear to be forced.

The group pursuits reported here are those I observed at close hand in either the focal territory or one immediately adjacent. Others heard on different parts of the garden but not observed directly are not reported. I

Table 1. Summary of observed copulations and courtships, including the responses of females to courtship

	Pair formation		Breeding Season			
	In-pair	Unforced extra-pair	In-pair	Unforced extra-pair	Group pursuits	Total
Copulations	0	1 (14%)	1 (14%)	3 (43%)	2 (29%)	7[1]
Courtships	2 (4%)	4 (9%)	3 (7%)	32 (71%)	4 (9%)	40[2]
Female response						
ignored or moved away	2 (100%)	2 (50%)	2 (67%)	26 (82%)	-	
"flirted"[3]	0	1 (25%)	0	2 (6%)	-	
copulated	0	1 (25%)	1 (33%)	3 (9%)	2 (50%)	
unknown	0	0	0	1 (3%)	2 (50%)	

1. 100% of copulations after pair formation and where the female cycle was known occurred during the females' presumed fertile period,

2. 84% of courtships after pair formation and where the female cycle was known occurred during the females' presumed fertile period,

3. female chased male for food in manner seen between paired birds.

observed the build up of two group pursuits during focal watches of the target female. In both cases extra-pair males were observed to congregate around the territory boundary, despite the efforts of the resident male to drive them off. I was unable to detect any trigger event that resulted in these extra-pair birds intruding simultaneously, but once they had, the resident male was unable to attack them all and a group pursuit of the resident female swiftly ensued.

Male courtship behaviour was more frequently observed than actual copulations (Table 1), and provided an indication of male copulation strategies, if not their outcome. Like copulations, the majority of observed courtships (71%) were by intruding males and were directed at resident females when the pair male was absent. After pair formation and where the female cycle was known, the majority (84%) took place when the female was presumed to be fertile.

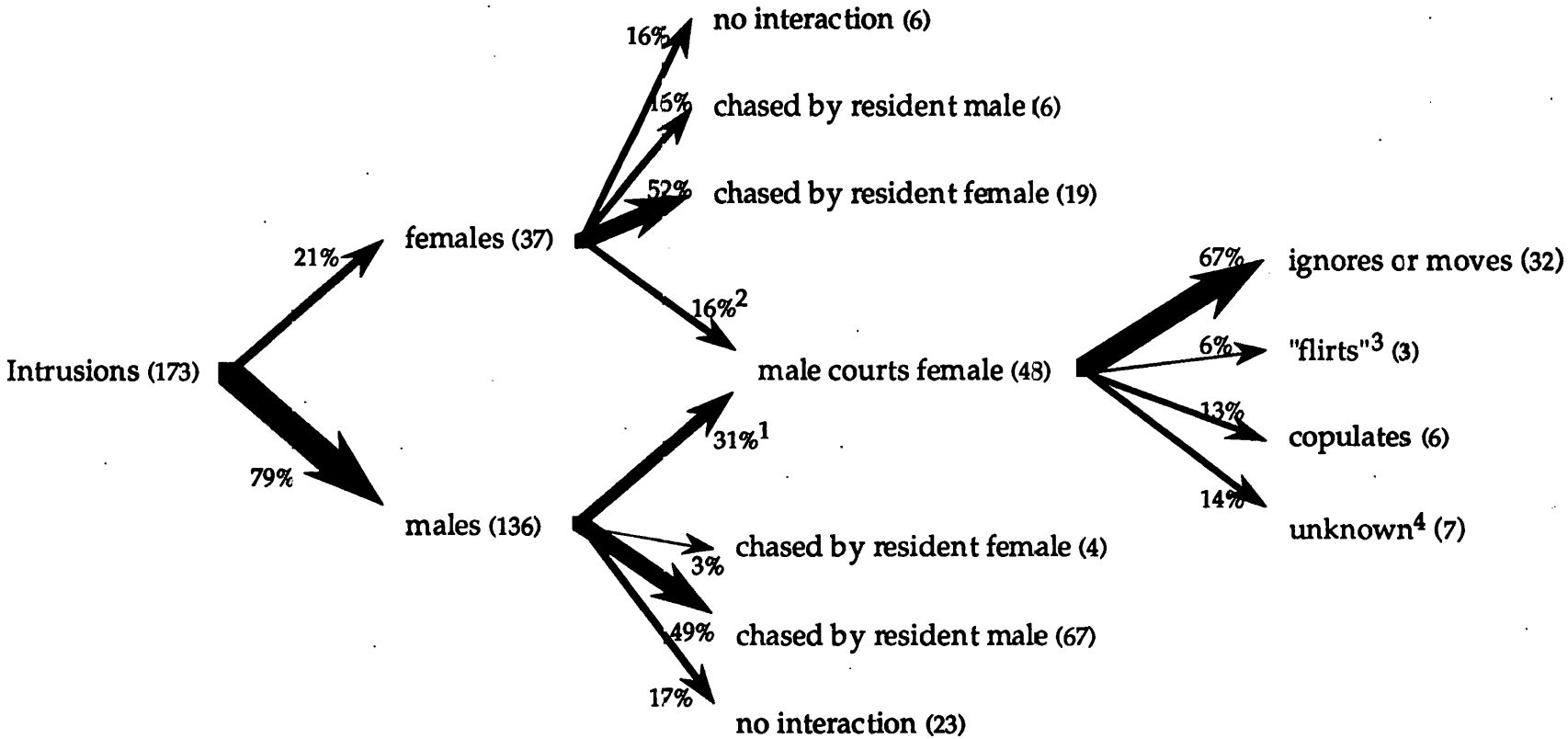
Females rarely responded to the courtship advances of intruding males (Table 1). Most frequently the courting male was ignored or the female flew away. Females were never seen to solicit copulations from intruding males without first being courted. When a female did respond, in all cases her mate was absent and apparently had no knowledge of the encounter.

Extra-pair intrusions

Although courtship and copulations were rarely observed, intrusions by extra-pair males were relatively common and accounted for 79% of the 173 recorded intrusion events (Figure 1).

Intruding males generally entered a territory with great stealth, often flying low between shrubbery or flower beds towards the resident female. A large proportion (49%) of observed extra-pair male intrusions were detected by the resident male and the intruder was aggressively chased from the territory, but in 31% of observed interactions the intruder approached the resident female to court her. Note that since many intruders were only

Figure 1. Observed incidence of territorial intrusions and the responses of the resident birds



1. includes four group pursuits assumed to consist of three pursuing males,
2. 5/6 interactions by one female who's territory overlapped two males,
3. female chased male for a morcel of food in a manner seen between paired birds,
4. copulation was likely but not actully seen, includes six group persuit males.

detected by the defensive reaction of the resident male, it is likely that these figures are an underestimate of the true frequency.

Other than one female whose territory came to overlap that of two males, only one incidence of a female approaching a male on another territory was observed. In general females remained on their territories, only occasionally making excursions over the boundary in search of a bathing sight or nesting materials, or when the pair were pushing to re-define a territory boundary near a new nest site.

The rate of both male intrusions and female intrusions did not change between the females' presumed fertile days and all other days of their cycles (Table 2). Nor, when considering the means over all days of the cycle for each pair in each year, were there any differences in the rates of intrusions between pairs due to either male age or female age (Table 3). However, as very few first year birds bred in the garden, the power of these analyses is low due to small sample sizes. Nevertheless, there is no suggestion in the data of type II error, with little difference between the medians of the samples and a large overlap in the variance in the data indicated by the IQRs.

There was no effect on intrusion rate of the resident male's bill colour or his body size or the body size of his mate (Table 4). Neither was the intrusion rate affected by the proportion of males in the study site who were not mate guarding (assuming days -5 until the laying of the penultimate egg of the clutch were spent mate guarding, Chapter Four) (Table 4).

For 37 intrusions, the identity of the intruding male was established and the breeding cycle of his mate was known. The frequency of such intrusions on the days when the male was guarding his own mate (days -5 until the laying of the penultimate egg of the clutch, Chapter Four) and on all other days of her cycle was compared to that expected if intrusions were randomly distributed, given the proportion of total watch time that spanned each stage. There was some indication that males intruded less than

Table 2. Summary of the rates of extra-pair male and female territorial intrusion behaviour and of female move initiation behaviour over the stages of the resident females' reproductive cycle. Data are presented as medians (+IQR) [range] with the results of Wilcoxon Signed Ranks test for 39 breeding attempts with matched data

	Presumed fertile days	All other days	Z	N^1	P
Male intrusions per hr	0.64 (3.60)	0.60 (2.09)	1.24	30	0.213
Female intrusions per hr	0.00 [5.28]	0.00 [1.72]	0.18	11	0.859
Proportion moves by female	0.47 (0.35)	0.27 (0.36)	2.55	38	0.011
Moves by female per hr	6.00 (7.81)	3.60 (5.45)	2.71	37	0.007
N	39	41			

1. after removing ties.

Table 3. Summary of the rates of extra-pair male and female territorial intrusion behaviour over all days of the females' reproductive cycle, and of resident female move initiation behaviour over the females' presumed fertile period, with the ages of the resident birds. Data are presented as medians (+IQR) over all attempts by each individual in each year. Statistics are Mann-Whitney U tests

	Male's age				Female's age			
	1st year	Older	*U*	*P*	1st year	Older	*U*	*P*
Over all days of females'cycle								
Male intrusions per hr	1.68 (0.69)	1.44 (2.04)	23.0	0.443	1.68 (0.78)	0.90 (1.98)	31.5	0.338
Female intrusions per hr	0.00 (0.13)	0.18 (0.48)	9.0	0.957	0.13 (0.47)	0.00 (0.43)	23.0	0.128
Over females' presumed fertile period								
Proportion of moves by female	0.45 (0.14)	0.44 (0.26)	26.0	0.920	0.49 (0.26)	0.40 (0.27)	28.0	0.322
Female moves per hr	6.67 (5.32)	7.09 (6.26)	26.0	0.920	8.64 (15.9)	5.53 (5.14)	25.0	0.215
N	3	18			5	16		

Table 4. Kendall's correlation coefficients between male bill colour index, male body size index and female body size index, and territorial intrusions over all days of the females' reproductive cycle and resident female move initiation behaviour over the females' presumed fertile period, for all attempts by each individual in each year; and with the proportion of neighbouring males who were not mate guarding for all attempts across all years. All *P*-values are >0.05

	Male bill colour	Male body size	Female body size	Total male pressure
Over all days of cycle				
Male intrusions per hr	0.000	-0.191	-0.252	-0.013
Female intrusions per hr	0.212	0.189	0.000	-0.037
Over females' presumed fertile periods				
Proportion moves by female	0.260	0.199	0.326	-0.020
Female moves per hr	0.087	0.126	0.079	0.005
N	15	17	16	41

Table 5. Observed frequency of male territorial intrusions with respect to their mate guarding behaviour, compared to that expected if intrusions were random, given the proportion of total watch time. $X^2=2.95$, $0.10>P>0.05$

	Stages of intruding male's reproductive cycle	
	Mate guarding days	All other days
Observed intrusions	7	30
Proportion of watch time	0.322	0.678
Expected intrusions	11.9	25.1

expected when they were mate guarding, but this was not statistically significant (Table 5).

Resident female movements

Females initiated more moves away from their mates during their presumed fertile period than during the rest of their reproductive cycles (Table 2). However, when considering the means over the females' presumed fertile periods for each pair in each year, there were no differences in female move initiation behaviour due to either male age or female age (Table 3); due to the resident male's bill colour, his body size or the body size of the female (Table 4), nor due to the proportion of males in the study site who were not mate guarding (see above) (Table 4).

DNA fingerprinting

Blood was taken from 8 broods, involving 5 different pairs and 19 chicks, and samples were run on three gels. Due to problems with enzyme digestion and poor quality fingerprints, fingerprints were obtained from 14 chicks in seven broods from four different pairs. Five chicks in two broods were compared with the fingerprints of both their putative parents, the remaining nine chicks in five broods with their putative mother only. Three broods had one or more nest mates' fingerprints missing. Bands lying between 5 and 23 kbases were scored for each fingerprint, with an overall mean of 37.0 bands per lane (SD=6.6, N=20, range 25 to 50).

Of the five chicks compared with both putative parents, three shared all their bands with one or both parents. A single unshared band in the fourth chick probably arose due to mutation (Bruford et al 1992). These data indicated that these four chicks were correctly assigned to their biological parents. The fifth chick, however, scored 5/31 (16.1%) bands which were present in neither parent, indicating that the parentage of this chick was not correctly assigned.

Band-sharing coefficients between the four correctly assigned chicks and their parents provided a mean band-sharing coefficient between first-

order relatives of 0.686 (*SE*=0.021), with 95% confidence intervals of 0.634 to 0.743. The mean band-sharing coefficients between 16 dyads of presumed unrelated individuals was 0.286 (*SE*=0.062), with 95% confidence intervals of 0.169 to 0.412.

The band-sharing coefficient of the excluded parentage chick with its putative mother was 0.730, and lay within the 95% confidence limits for known parents and offspring, indicating that maternity was correctly assigned. The band-sharing coefficient with its putative father was 0.369 and lay within the limits for coefficients between presumed unrelated individuals, indicating that the chick was not fathered by the male who attended the nest. (Figure 2).

Of the nine chicks compared with their putative mother only, the band-sharing coefficients of each chick and its putative mother were not statistically different from those of known offspring and parents (Student's t test after arcsine transformation, t_{11}=0.09, P=0.927; Figure 2), indicating that maternity was correctly assigned. Although the fingerprints of these chicks could not be compared with that of their putative father, a comparison with their nest mates provided an indication of their relatedness. Since all maternity was correctly assigned, coefficients of less than that expected between first-order relatives indicated extra-pair paternity.

The band-sharing coefficients between 10 dyads of nest mates in 4 broods, fell within the range expected for first-order relatives (Figure 2) and were not statistically different from the coefficients of known parents and off-spring (t_{12}= 1.67, P=0.121) indicating that these chicks were all full siblings of their nest mates. Although technically possible, it is highly unlikely that all the chicks in every one of these four broods were fathered by the same extra-pair male as their siblings, and it is most probable that these chicks were fathered by the male who attended the nest.

Two chicks in one brood had a band-sharing coefficient that fell below the 95% confidence limits of first-order relatives (Figure 2). Since both these

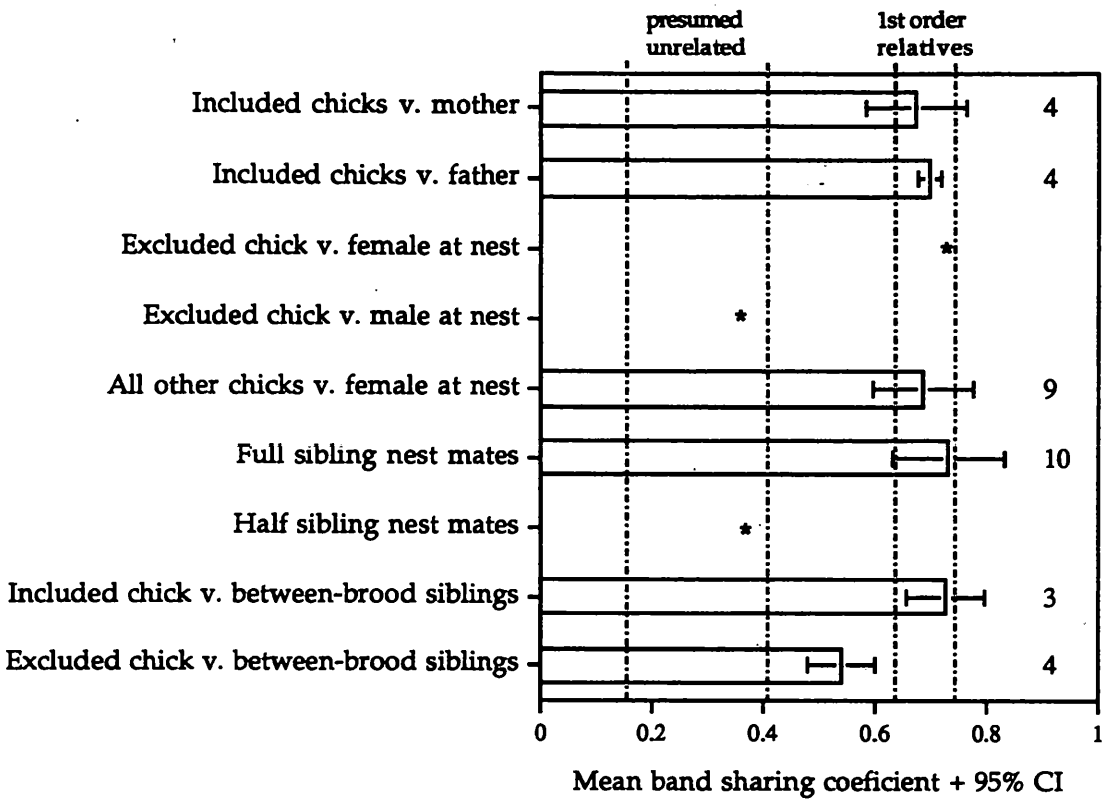


Figure 2. Summary of band-sharing coefficients between off-spring and the adults who attended the nest, nest-mates, and between-brood off-spring of the same pair. Data bars are mean coefficients and 95% CI with the number of dyds indicated. Asterixes are band sharing co-efficients for single dyads. The dotted lines indicate the 95% CI limits for presumed unrelated individuals and for known first-order relatives.

chicks had correctly assigned maternity, this indicated that they were fathered by different males. Other broods from the same pair were available on the same gel and comparisons of close lanes from the different broods provided band-sharing coefficients for between-brood siblings. One chick could be compared with three between-brood siblings and generated band-sharing coefficients with that fell within the 95% confidence limits for first-order relatives. These were not statistically different than to those for known first-order relatives (t_5=1.85, P=0.123) and indicated that it was a full sibling of these other broods. The other could be compared with four between-brood siblings and generated band-sharing coefficients that fell below the lower 95% confidence limit for first-order relatives. These coefficients were statistically smaller than those for known first-order relatives (t_6=7.58, 1-tailed P=0.000) and statistically larger than those for the presumed unrelated individuals (t_{18}=7.11, 1-tailed P=0.000), indicating that this chick was a half-sibling of these other broods. Hence one chick had within-pair paternity and the other extra-pair paternity (Figure 2).

Discussion

Although very few copulations were observed where both birds could be identified, those that were suggested that EPCs occurred during the females' presumed fertile period and had the potential to play an important role in the birds' reproductive strategies (Table 1). The results from the DNA fingerprinting exclusion and band-sharing coefficients analyses, indicated that all of the chicks who were fingerprinted were the offspring of the female who attended the nest, but two out of the 14 chicks from two out of seven broods were fathered by extra-pair males (Figure 2). These data confirmed that extra-pair paternity occurred in this population.

There was no behavioural or genetic evidence to suggest intra-specific brood parasitism.

Males were commonly observed to intrude onto the territories of their neighbours to court the resident female (Figure 1). Occasionally, where several males intruded onto a territory simultaneously, females were subjected to group pursuits with attempted FEPCs (Table 1). These data suggest that, in common with many other territorial passerine species, male European blackbirds seek extra-pair paternity by intruding onto the territories of their neighbours in search of EPCs (eg Buitron 1983, Westneat 1988, Hanski 1992, Stutchbury 1998). When intruding alone males attempt to court the resident female, but when several males intrude together they may attempt to force copulations upon her, though the reproductive value of these copulations remains in doubt (Fitch & Schugart 1984, Gowaty & Buschhaus 1998).

Females were rarely observed to leave their territory, were never seen to approach or solicit copulations from extra-pair males and only rarely appeared to accept the courtship advances of intruding males (Figure 1). Females did initiate more moves away from their mate during their presumed fertile period (Table 2) and this has been interpreted in other species as attempts by females to escape male mate guarding in order to copulate with other males (Birkhead 1979, Davies 1992, Sheldon 1994a). These data suggest that female European blackbirds do not overtly seek or solicit EPCs, but do perhaps move within their territory to increase the opportunity of being approached by intruding males. However, the possibility that females made covert extra-territorial forays to seek EPCs cannot be entirely discounted without radio tracking, but the detailed observations made in the open habitat of this study suggest this is unlikely in this species.

Females appear to control the outcome of extra-pair courtship by choosing to either accept or reject male courtship advances (Figure 1) (Birkhead et al 1988a, Møller 1988, Burley et al 1994, Mills 1994, Stutchbury &

Neudorf 1998). However, females may be unable to avoid FEPCs when several males force the female to the ground during a group pursuit.

Unlike other socially monogamous passerines (see Birkhead & Møller 1992), males did not appear to target their territorial intrusion behaviour at females who were likely to be fertile (Table 2). This suggests that males were unable to determine the fertility status of females from a distance, since it is unlikely that a male would risk leaving his own territory undefended and run the gauntlet of another male's territorial aggression to approach a known unfertile female. However, males do appear to be able to determine fertility from a close distance, since resident males begin mate guarding before egg laying begins (Chapter Four). Indeed all observed copulations and group pursuits during the breeding season occurred during the female's presumed fertile period.

Intruding males did not appear to target the territories of younger, smaller or less brightly coloured males (Tables 3 & 4), which as potential indicators of quality (Andersson 1994), may have indicated males who were less able to detect and oust intruders.

This lack of selectivity in male intrusion behaviour may be explained by the very high predation rate in this, and other reported populations of blackbirds (see Introduction), which introduces a large element of chance into raising a brood successfully and so reduces any advantage in being selective. By quite literally attempting to put eggs in as many baskets (nests) as possible, males increase their chances of achieving at least some reproductive success even if their clutches at home all fail (Perreault et al 1997). This may also explain why males continue to engage in EPC attempts when mate guarding their own presumed fertile female (Table 5), despite the increased risk of cuckoldry it is likely to entail (Birkhead & Møller 1992).

Over-all, male territorial intrusion behaviour appears to be opportunistic, with subjective observations in the field suggesting that males attempt intrusions whenever they perceive the opportunity to

approach a neighbouring female without being detected and ousted by the resident male. However, the majority of extra-pair courtship and all extra-pair copulations observed during the breeding season were directed at presumed fertile females.

Females, on the other hand, were apparently much less pro-active in their EPC tactics, which appeared to be limited to occasionally responding to the courtship advances of intruding males (Table 1). When females did accept the advances of males, it was generally in the close confines of dense vegetation. This secretive nature of courtship and copulation by blackbirds, both within and outside pair-bonds, may be a tactic to avoid group pursuits, as birds engaging in overt sexual behaviour attract interference from neighbouring males (Snow 1958b, pers obs).

Westneat (1992) suggests that when female birds do not incite EPCs, but appear merely to accept or resist them, then females may be pursuing either a mixed reproductive strategy by accepting some males when the benefits of copulating outweigh the costs (eg Björklund et al 1992, Lifjeld and Robertson 1992, Mills 1994, Dickinson 1997); or be pursuing a "best of a bad job" strategy (Trivers 1972, Dawkins 1976) when the costs of rejecting some males' advances outweigh the benefits (eg Røskaft 1983, Frederick 1987a). Since females appeared to control the outcome of unforced EPC advances, and vigorously resisted FEPC attempts, it is unlikely that females passively took part in EPCs to avoid the costs of rejecting some males as a "best of a bad job" strategy. But the lack of overt encouragement or seeking of EPCs suggests that the benefits of more apparent EPC tactics do not outweigh the costs.

The potential non-genetic benefits to females of more pro-active EPC tactics appear slim, since blackbirds do not engage in courtship feeding and females rarely venture from their own territories to benefit from the resources offered on the territories of EPC males (Gray 1997b). Even when dry weather forces the birds to forage off-territory, non-defended areas of

open habitat tend to be used (Snow 1958b, Edwards 1983, pers obs). However, between 8-10% of blackbird eggs fail without any apparent embryo development (Magrath 1989, E. Creighton unpublished data) and females may engage in EPCs to insure against low sperm counts in their mate (Wetton & Parkin 1991, Wagner 1991a, Sheldon 1994b, Gray 1997a, but see Birkhead et al 1995). Females may also take part in EPCs with high quality males to increase the genetic quality of their off-spring when they are paired to low quality males (Birkhead & Møller 1993, Gowaty 1996), since the choice of mate at pair formation is limited by intra-sexual competition for high quality habitat (Chapter Six). However there was no indication that females paired to younger or smaller males or males with less brightly coloured bills, made more moves away from their mate's mate guarding attentions (Tables 3 & 4). Also, the case for genetic benefits to females is heavily confounded by the high nest predation rate in European blackbirds, which will dilute any sexual selection pressures that such female choice for EPC males may have.

In contrast to the few likely increases in benefits to females of more pro-active EPC tactics, the major potential costs of EPCs are likely to increase with more visible extra-pair sexual behaviour. Firstly, female blackbirds are highly dependent upon the parental care contribution of their mate for fledging success. Blackbird chicks are unable to thermoregulate in the first few days after hatching and require brooding from the female while the male is responsible for the bulk of food collection (Snow 1958a, 1958b). Indeed widowed females rarely succeed in raising any offspring (R. Magrath pers. comm.). So it is possible that females refuse EPC opportunities in order to ensure their mate's confidence of paternity (Whittingham et al 1992, Westneat & Sherman 1993).

Whilst there is some evidence that males of some species do reduce their parental care contribution when faced with reduced confidence of paternity (eg Burke et al 1989, Davies 1992, Dixon et al 1994, Wright & Cotton 1994), in others there is no correlation (eg Gavin & Bollinger 1985, Frederick

1987b, Westneat 1995, Whittingham et al 1993, Wagner et al 1996a). In a recent review of the debate, Gowaty (1996) concludes that where there are no alternative helpers or the female is unable to compensate for the reduction in male parental care, both males and females suffer a reduced reproductive success from any male withdrawl of care and the male has no alternative but to continue to provide care to broods that may contain both his own and extra-pair young (Maynard-Smith 1977, Graffen 1980).

Since male parental care appears to be essential for reproductive success in European blackbirds, here males may not have the option of constraining female extra-pair sexual strategies by the threat of withdrawl or reduction of their parental care. In support of this conclusion, Table 6 (page 29) summarises the literature where female EPC tactics have been described and shows that there is no correlation between the degree of overtness of female tactics and breeding system, where breeding system is taken as a broad indicator of the degree of dependence upon male parental care of reproductive success (Emlen & Oring 1977).

A second potential EPC cost to females that will increase with more visible extra-pair sexual behaviour, is that overt solicitation and copulation attract any male in the vicinity who then interferes with the copulation attempt (Snow 1958b, pers obs). If males arrive in sufficient numbers to overwhelm the resident male's defensive behaviour then the female risks being chased and attacked by males attempting to force copulations. In this population of blackbirds, females may not use overt EPC tactics in order to avoid inducing aggressive pursuits by groups of intruding males. Although this may reduce the number of lone males attracted to court the female, it minimises the costs of injury and stress likely to be associated with group pursuits. A review of the literature where female EPC tactics have been described supports this interpretation (Table 6).

In species where female tactics are described as only accepting or rejecting the courtship advances of intruding males (Table 6a) all have

reports of females being subjected to FEPC attempts, with the exception of the feral pigeon where the authors report sexual harassment and aggression from extra-pair males, but not FEPC. In species where females are observed to overtly encourage or seek EPCs on extra-territorial forays (Table 6b), there are no reports of FEPCs in 19 out of the 21 species described. Ultimately the costs associated with FEPCs may be a major limiting factor on the range of extra-pair sexual tactics adopted by females in this and other species. However, this may not necessarily constrain female extra-pair sexual strategies, as more covert tactics that are not detected by either human observers or male conspecifics may be employed to overcome this constraint.

In summary, both male and female European blackbirds adopt EPC strategies. Males appear to make opportunistic intrusions onto the territories of their neighbours and attempt to court resident females during their fertile periods. Forced EPCs are attempted when several intruding males overwhelm the resident male's guarding behaviour and invade the territory to chase the resident female. The high predation rate on blackbirds' nests may promote male extra-pair strategies, as by fertilising eggs in as many nests as possible, he increases his chances of achieving some paternity success. Female tactics appear to be limited to occassionally accepting unforced EPCs from intruding males who succeed in avoiding detection by the resident male. This suggests that the costs of more overt tactics outweigh the benefits. The potential for material benefits are limited and the high rate of predation dilutes potential genetic benefits. However, the potential costs are likely to increase with more overt tactics. A review of the liturature where female EPC tactics are described supports the conclusion that the potential loss of male parental care does not constrain the overtness of female tactics, but that the risk of stress and injury from FEPC attempts by nearby males attracted by overt sexual behaviour does.

Table 6. Species where female EPC tactics have been described, whether FEPCs have been reported and their breeding system.

a) species where female tactics are limited to rejecting or accepting the courtship advances of extra-pair males

Species	Female tactic[1]	FEPC?[2]	Breeding system[3]	Reference
White ibis	Reject	Yes	Monogamous	Frederick 1987a
Lesser snow goose	Reject	Yes	Monogamous	Dunn et al 1999
Ross's goose	Reject	Yes	Monogamous	Dunn et al 1999
White-cheeked pintail	Reject	Yes	Monogamous	Sorenson 1994
Green-winged teal	Reject	Yes	Monogamous	McKinney & Stolen 1982
Red-billed gull	Reject	Yes	Monogamous	Mills 1994
Feral pigeons	Reject	No[4]	Monogamous	Lovell-Mansbridge & Birkhead 1998
White fronted bee-eater	Reject	Yes	Monogamous	Emlen & Wrege 1986
Barn swallow	Reject	Yes	Monogamous	Møller 1985, 1988
Purple martin	Reject	Yes	Monogamous	Brown 1978, Wagner et al 1996b
Western bluebird	Reject	Yes	Monogamous	Dickinson 1997
European blackbird	Reject	Yes	Monogamous	Creighton, this study
Wheatear	Reject	Yes	Monogamous	Currie et al 1999

Yellow warbler	Reject	Yes	Monogamous	Yezerinac & Weatherhead 1997
Pied flycatcher	Reject	Yes	Polygynous	Alatalo et al 1987, Björklund & Westman 1983
Indigo bunting	Reject	Yes	Polygyny	Westneat 1987
Red-winged blackbird				
Eastern population	Reject	Yes	Polygyny	Westneat 1992
House sparrow	Reject	Yes	Monogamous	Møller 1987, 1990
Northern oriole	Reject	Yes	Monogamous	Edinger 1983
Rook	Reject	Yes	Monogamous	Røskaft 1983

1. female tactics after Stutchbury & Neudorf (1998)
2. whether observations of forced copulation attempts on females by extra-pair males have been reported
3. social breeding system, where polygyny includes facultative polygyny
4. no FEPC reported, but females suffer sexual harassment and aggression by extra-pair males.

b) species where female tactics include the encouragement of advances from EPC males by overt solicitation or advertisement of fertility and the active seeking of EPCs by visiting chosen males on their territories (or mating area)

Species	Female tactic[1]	FEPC ?[2]	Breeding system[3]	Reference
Northern fulmar	Rejection; Foray	No	Monogamous	Hatch 1987
Blue footed booby	Solicit	No	Monogamous	Osorio-Beristain & Drummond 1998
Shag	Foray	No	Monogamous	Graves et al 1993
Crested auklet	Reject; Foray	No	Monogamous	Hunter & Jones 1999
Least auklet	Reject; Foray	No	Monogamous	Hunter & Jones 1999
Parakeet auklet	Reject; Foray	No	Monogamous	Hunter & Jones 1999
Whiskered auklet	Reject; Foray	No	Monogamous	Hunter & Jones 1999
Common guillemot	Reject; Solicit	Yes	Monogamous	Birkhead et al 1985, Hatchwell 1988
Razorbills	Reject; Foray	No	Monogamous	Wagner 1991c, 1992a
Tree swallow	Reject, Foray	No	Polygynous	Lifjeld & Robertson 1992, Venier et al 1993
Bluethroat	Foray	No	Polygynous	Smiseth & Amundsen 1995
Eastern bluebird	Foray	No	Monogamous	Gowaty & Bridges 1991

Hooded warbler	Solicit; Foray	No	Monogamous	Neudorf et al 1997
Seychelles warbler	Solicit	No	Monogamous	Komdeur et al 1999
Bearded tit	Reject; Solicit	No	Monogamous	Hoi 1997
Black-capped chickadees	Foray	No	Monogamous	Smith 1988, Otter et al 1994
Blue tit	Reject; Foray	No	Polygynous	Kempenaers et al 1992, Kempenaers et al 1995
Great tit	Reject; Foray	No	Monogamous	Björklund et al 1992, Otter et al 1999
Red-winged blackbird				
Western population	Reject; Foray	No	Polygyny	Gray 1996
Chaffinch	Solicit; Foray	No	Monogamous	Sheldon 1994a
Zebra finch	Reject; Solicit	Yes	Monogamous	Birkhead 1988, Birkhead et al 1989, Burley 1994, Houtman 1992

1. female tactics after Stutchbury & Neudorf (1998)
2. whether observations of forced copulation attempts on females by extra-pair males have been reported
3. social breeding system, where polygyny includes facultative polygyny

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Chapter Four: Paternity protection tactics in the European blackbird

Paternity protection behaviour is well documented in passerine bird species. However it is potentially costly in time and energy, and males are expected to fine tune their strategies to reflect variation in their risk of losing paternity. This paper describes how male European blackbirds, Turdus merula, *attempt to protect their paternity by both mate guarding and territorial defence, and explores how the intensity of these vary in relation to female fertility and the risk of loss of paternity. Pair proximity and territorial behaviour of the population in the Oxford Botanic Garden were recorded over three breeding seasons. The intensity of mate guarding varied relatively to presumed female fertility and was most intense in the days immediately before and during egg laying, when the female was most likely to be fertile. First year males guarded more intensely than older birds and there was some suggestion that males of all ages guarded more intensely with increases in the proportion of neighbouring males who were not mate guarding their own female. Territorial defence remained constant throughout the reproductive cycle, but was combined with mate guarding by the male perching above the female and seemingly combining surveying his territory with monitoring the female's activities. Male mate guarding appears to serve the primary function of preventing the pair-female from participating in EPCs, whilst territorial defence appears to serve the primary function of excluding other males from gaining access to the pair female.*

Introduction

Since Trivers (1972) made his famous prediction that monogamously mated males should pursue mixed reproductive strategies, a wealth of evidence has been collected from a wide range of bird species that show males do indeed attempt to fertilise the eggs of females mated to other males, whilst also trying to ensure their paternity of the off-spring of the female they are paired to (Birkhead & Møller 1992a; Birkhead 1998). In a comparative analysis of the literature, Møller and Birkhead (1991) identified two broad strategies used by males to ensure their paternity. Where ecological conditions permit, males employ pre-copulatory paternity protection tactics to prevent copulations between their mate and other males for the duration of viable sperm storage and egg fertilisation. In other situations, males employ apparently less successful post-copulatory strategies, usually multiple within-pair copulations to swamp any extra-pair males' sperm and reduce the probability of them fertilising the females' eggs.

Engaging in paternity protection behaviour is costly in both time and energy and may conflict with other behaviour (Møller 1987a; Lamprecht 1989; Davies 1992; Westneat 1994). Males are therefore expected to fine tune their strategies to reflect variation in their risk of losing paternity (Møller 1985). This risk will not be constant across the females' cycle, and paternity protection behaviour should be timed to coincide with female fertility (Birkhead & Møller 1992a; Birkhead 1998). However, fertilisation success appears to depend not only upon the timing of ovulation, but also upon the timing of copulations, the relative numbers of sperm inseminated by pair and extra-pair males, and the duration and effectiveness of sperm storage by the female (Birkhead & Møller 1992a; Birkhead et al 1995; Colegrave et al 1995; Birkhead 1998).

The risk of lost paternity may also vary with the likelihood of females engaging in extra-pair copulations (EPCs). This may differ between

individuals due to both variation in their encounter rate with extra-pair males (eg Møller 1985; Alatalo et al 1987; Birkhead & Biggins 1987; Weatherhead 1997), and in the likelihood of the female accepting or rejecting the advances of extra-pair males (Møller 1992; Lifjeld et al 1994; Dickinson 1997; Petrie & Kempenaers 1998). Where extra-pair paternity offers fitness benefits to females, then the attractiveness of the potential extra-pair male relative to the pair male may influence the likelihood of females to engage in EPCs (eg Smith 1988; Kempenaers et al 1992; Kempenaers et al 1995; Sunberg & Dixon 1996; Saino et al 1997; Johnsen et al 1998).

In the European blackbird (*Turdus merula*), copulations are rare and males are readily observed in close association with their mates during nest building and egg laying (Snow 1958a). Therefore, it is likely that in common with the majority of solitary, territorial passerines (Birkhead & Møller 1992a; Birkhead 1998), male blackbirds adopt mate guarding by close association (Beecher & Beecher 1979; Birkhead 1979) as their primary paternity protection tactic.

In my study population in the Oxford Botanic Garden, extra-pair copulations were occasionally observed (6/7 observed copulations were with extra-pair males) and territorial intrusions by neighbouring males to court the resident female were common (2.05 intrusions per hour during the females' likely fertile periods). Although females rarely left their territory, were never seen to solicit males and appeared to reject the majority of EPC advances, DNA fingerprinting analyses indicate that extra-pair paternity occurs (14% (2/14) of chicks and 29% (2/7) of broods) and males are at risk of losing their paternity to other males (Chapter Three).

This paper describes the types of, and variation in the paternity protection tactics of the Oxford Botanic Garden blackbirds and discusses whether these reflect fine tuning of male strategies in relation to their risk of loss of paternity.

Methods

I observed colour-ringed blackbirds in Oxford Botanic Garden (51°44'N,1°16'W), Oxfordshire, UK, from February to mid June 1991-93. In total sixteen different male-female pairings were followed, involving 12 males and 13 females. Most individuals were captured yearly in Potter traps (Davis 1981), were aged and sexed by plumage characteristics (Snow 1958a). Morphological measurements (Spencer 1984; Yezerinac et al 1992) and estimates by eye of the percentage of the bill coloured yellow-orange were made. From March 1991 the richest tone of bill colour was matched in daylight to Pantone colour cards (Letraset by Pantone © 1990).

An index of body size for each bird in each year was calculated from principal components analysis of wing-length and tarsus-length. The PC1 scores derived explained 72.0% of the variance with character loadings of 0.85 for both measures. T score transformation converted these into positive integers (Howell 1992). An index of bill colour for each individual in each year was calculated using derivatives from the seasonal maximum of percentage of the bill coloured orange/yellow, multiplied by the rank of the colour from yellow to orange made by three naive observers from the 16 Pantone colour codes used in the study.

Each nesting attempt was observed from nest-building to fledging or until the attempt was lost, with the majority of observations concentrated on the days leading up to and including egg-laying. Data were collected at all times during daylight hours, with a peak between 6am and 11am BST. Observations began when a focal pair were located on their territory and lasted for 20 minutes or until the birds were lost from view for two consecutive minutes. Mean watch duration was 18.3 minutes, with an average of 5.5 watches per attempt and a total observtion time of 67.41 hours. The birds were watched from the periphery of their territory with no attempt at concealment, since they were habituated to human presence. The order in which the pairs were watched was random on each field day.

Specific behaviour recorded was as follows. At one minute intervals estimates were made of 1) intra-pair distance in metres, 2) whether the pair were in visual contact, and 3) the height in metres above ground of each focal bird. When a bird was out of visual contact with its mate (eg over a wall or on the other side of the territory), a distance of >25 m was recorded. Further behaviour was recorded as it occurred. 4) Initiation of moves of a distance greater than 5m or out of perceived visual contact with the mate, and whether the mate followed within 30 seconds. 5) Rendezvous moves to within 10 m and perceived visual contact of the mate, made after the pair had been separated for longer than one minute and/or had been involved in independent activities. 6) Duration of boundary patrols by the male. These included display flights between vantage points around the periphery of the territory, and trips to oust intruders or to engage in boundary disputes with neighbours. 7) Territory boundary displays (Snow 1958a) or fights.

Data were collected over 41 nesting attempts where the date of clutch initiation was known (37% first attempts, 39% second, 22% third and 2% fourth attempts). The date of clutch initiation and the final clutch size were determined from nest checks. Two nests were not found until after egg laying, and the date of clutch initiation was estimated from the day the chicks hatched, 13 days after the last egg was laid (Snow 1958a, 1958b). Fledgling success was low (27% of nests in which a clutch was initiated fledged young, Chapter Two) and not all pairs succeeded in raising young. Across all three seasons, only three further nesting attempts were made following the successful fledging of a brood.

The data were organised in relation to the day of the females' reproductive cycle so that day zero corresponded to the day the first egg was laid. This permitted direct comparisons of different breeding attempts from different calendar dates. The females' cycle was then divided into four stages based upon observations of behaviour and theoretical expectations. These stages were defined as follows. *Pre-fert:* days up to and including the sixth

day (day -6) before the first egg was laid. This is prior to the earliest day that breeding copulations have been recorded in blackbirds (though copulations may occur earlier in the year during pair formation) (Snow 1958a, pers obs). For first attempts this period began as soon as a breeding pair was established (Snow 1958a), for replacement attempts it began the day after the previous attempt was lost and for second broods it began eleven days before the initiation of the next clutch. *Fert:* between five and two days before the first egg was laid (days -5 to -2). This was prior to ovulation and fertilisation (see below), but included the period in which copulations have been recorded in blackbirds (Snow 1958a, pers obs). Given that the duration of sperm storage in birds is six days or longer (Birkhead & Møller 1992b), sperm inseminated during copulations in this period could fertilise eggs during the forthcoming laying sequence. *Egg-fert:* from the day before the first egg was laid until the day the penultimate egg of the clutch was laid. Given that fertilisation occurs 24 hours before each egg is laid (reviewed in Birkhead 1998), the female was fertile on these days. *Inc & brood:* including the day the last egg was laid, 13 days of incubation and 13 days of brooding (Snow 1958a, 1958b).

The majority of data were not normally distributed and not readily amenable to transformation, so non-parametric statistical treatments are used throughout unless otherwise stated. Rates of behaviour per minute were derived from the duration of the watch and when combining data from several watches, averages were weighted by watch duration.

Results

Pair association behaviour

Intra-pair distance varied over the stages of the females' reproductive cycle (Table 1), decreasing to a minimum from five days before the first egg was laid until the laying of the penultimate egg, after which it increased. This decrease in intra-pair distance was associated with the peak in the

Table 1. Summary of the changes in male mate guarding behaviour and male territorial defense behaviour over the stages of the females' reproductive cycle. Data are presented as medians (+IQR) or [range] for N attempts. Friedman two-way ANOVA results are for 27 breeding attempts with data available for all four stages

	Pre-fert	Fert	Egg-fert	Inc & brood	*Fr*	*P*
Mate Guarding						
Intra-pair distance (m)	14.60 (7.89)	8.56 (5.00)	9.67 (7.85)	17.00 (4.95)	34.97	0.000
Male follows female	0.12 (0.31)	0.57 (1.00)	0.30 (0.67)	0.00 (0.00)	13.67	0.003
Female follows male	0.00 [0.00]	0.00 [0.39]	0.00 [0.50]	0.00 [0.20]	1.13	0.988
Male rendezvous	0.21 (0.67)	0.63 (1.0)	0.20 (0.55)	0.25 (0.52)	2.78	0.427
Visual contact	0.95 (0.24)	0.94 (0.15)	0.92 (0.19)	1.00 (0.17)	2.17	0.539
Territorial Defence						
Male perch height (m)	1.25 (1.19)	2.80 (2.54)	2.45 (3.45)	2.20 (3.35)	2.66	0.448
Proportion time patrolling	0.03 (0.13)	0.05 (0.15)	0.09 (0.19)	0.00 (0.12)	2.17	0.539
Rate boundary disputes (min^{-1})	0.00 (0.03)	0.00 (0.05)	0.00 (0.05)	0.00 (0.03)	2.99	0.393
N	39	39	32	27	df = 3	

For inter-pair distances, the differences lie between the Prefert and Fert stages, and the Eggfert and Inc & Brood stages, at α=0.05. For the proportion of female moves followed by the male, the difference lies between the Prefert and Fert stages, at α=0.05.

proportion of female-initiated moves followed by the male, but not with any changes in the proportion of male-initiated moves followed by the female (Table 1). The proportion of moves made by the male which brought the pair members together, and the proportion of time the pair spent in visual contact did not vary with the stages of the female's reproductive cycle (Table 1).

Following Davies and Hatchwell (1992; Hatchwell and Davies 1992), these analyses assumed that data collected from each breeding attempt were independent. Although six pairs contributed only one attempt, ten contributed two or more (range 2 to 7, median 2.4). However, the variation in the intensity of paternity assurance measures between these pairs was no greater than that exhibited by the individual pairs over repeated attempts, indicating that the data were not biased by these repeated measures (1-way ANOVA: intra-pair distance after $\log_{10}$ transformation, $F_{9,34}=1.19$, $P=0.347$; male follows female after arcsine transformation, $F_{9,34}=1.47$, $P=0.212$).

An alternative method of addressing this potential problem of pseudoreplication is to conduct conservative analyses of the paternity assurance measures using data from only one attempt for each pair (chosen as the attempt with most data across the four stages). These analyses show similar results to the full analyses and indicate that the data were not biased by these repeated measures (Friedman two-way ANOVA: intra-pair distance, $Fr_3=24.12$, $P<0.001$; male follows female, $Fr_3=8.94$, $P=0.030$; female follows male, $Fr_3=0.170$, $P=0.982$; male rendezvous, $Fr_3=2.99$, $P=0.395$, visual contact $Fr_3=3.28$, $P=0.351$). However, the method following Davies and Hatchwell above is the one established in the literature and on that basis is my preferred method.

A second potential source of error arises from treating each unique male and female combination as statistically independent even though some birds were included twice when with different partners in different years. However, conservative analyses of the paternity assurance measures

using data from each individual in only one pairing (after Davies & Hatchwell 1992) show similar results as the full analyses and indicate that the data were not biased by repeated measures (Friedman two-way ANOVA: intra-pair distance, Fr_3=27.81, P<0.001; male follows female, Fr_3=10.07, P=0.018; female follows male, Fr_3=0.171, P=0.982; male rendezvous, Fr_3=2.97, P=0.396, visual contact Fr_3=1.64, P=0.649).

Males did not normally associate with their mate on the ground, but typically perched above her from where they appeared to combine vigilance of the female with monitoring of their territory (median (IQR) perch heights in meters across all stages of the females' cycle: males 2.23 (1.72); females 0.56 (0.75); for 16 pairs, Wilcoxon Signed Ranks Test, Z_{16}=3.46, P<0.001).

Territorial Defence

Males maintained the integrity of their territories throughout each breeding attempt with constant vigilance, vigorous defence of their boundaries and the ousting of intruders (Snow 1958a, pers obs). Møller (1990) has suggested that territorial defence serves as a paternity guard by preventing the access of other males to the female, and males might be expected to engage in higher levels of territorial defence during the females' fertile period. However, there was no variation over the stages of the females' reproductive cycle in either male perch height, the proportion of time males spent patrolling their territory boundaries nor the rate at which they engaged in boundary disputes (Table 1), indicating that males maintain an equal intensity of territorial defence independently of female fertility.

Variation Due to Male Age

To test for the effect of male age on pair association behaviour, first year males were compared with those of two years and older. Over the Fert and Egg-fert stages for all attempts by each individual in each year, first year males maintained a closer distance to their mate and had a not quite statistically significant tendency to follow more of her moves than older males (Table 2). However with only three first year males breeding on the

Table 2. Summary of the differences in male mate guarding behaviour and male territorial defense behaviour between first year and older birds. Data are presented as medians (+IQR) over the Fert and Egg-fert stages for all attempts by each individual in each year. Statistics are Mann-Whitney U tests

	1st yr male	Older male	*U*	*P*	1st yr female	Older female	*U*	*P*
Mate Guarding								
Intra-pair distance (m)	7.83 (5.59)	9.40 (3.82)	6.0	0.035	7.85 (6.40)	9.15 (1.37)	31.0	0.457
Male follows female	0.75 (0.38)	0.48 (0.52)	9.0	0.069	0.58 (0.72)	0.50 (0.54)	35.5	0.709
Male rendezvous	0.75 (0.12)	0.49 (0.54)	14.0	0.190	0.72 (0.44)	0.49 (0.45)	32.5	0.534
Visual contact	0.92 (0.12)	0.86 (0.17)	23.0	0.687	0.91 (0.27)	0.86 (0.17)	37.0	0.804
Territorial Defence								
Male perch height (m)	1.43 (2.18)	2.47 (2.45)	21.0	0.547	2.50 (2.58)	2.08 (2.53)	37.0	0.804
Proportion time patrolling	0.15 (0.11)	0.12 (0.15)	23.5	0.724	0.26 (0.18)	0.12 (0.16)	29.5	0.384
Rate boundary disputes (min^{-1})	0.01 (0.02)	0.01 (0.03)	22.5	0.642	0.01 (0.03)	0.01 (0.02)	37.0	0.799
N	3	18			5	16		

site, the power of this statistical test is low (>80% chance of a type II error). There was no statistically significant difference, nor any indication in the data, in the proportion of pair-rendezvous moves made by the male nor in the proportion of time the pair members were within visual contact (Table 2).

There was no difference in any of these variables between first year and older females (Table 2). Again low statistical power may also account for these lack of statistical differences. However, from the data available (Table 2) there is little suggestion of any real differences as for all three measures the degree of overlap of the scores, as indicated by the IQRs, is much larger than any differences between the medians.

Variation Due to Male Bill Colour and Body Size

To test for the effect of male bill colour on pair association behaviour, correlations of each measure over the Fert and Egg-fert stages for all attempts by each individual in each year, were made against the index of bill colour. Of the 15 males for whom full bill colour data was available, there was no relationship between bill colour and any of the measures of either mate guarding or territorial defense behaviour (Table 3). Similar correlations made against the indices of body size indicated no over-all effect of either male or female body size on measures of mate guarding or territorial defense (Table 3).

Effects of Breeding Asynchrony

Assuming that males guard their mates over Fert and Egg-fert stages of the females' cycle and seek extra-pair copulations at other times (Chapter Three), in an asynchronously breeding population the number of males seeking EPCs at any one time will vary. Not all males will necessarily be acceptable to all females as potential EPC partners, but as an index of the risk of cuckoldry posed by the available males, the proportion of non-guarding males in the study site was calculated for each pair on each day of each breeding season (total male pressure, TMP). For territories on the edge of the

Table 3. Kendall's correlation coefficients between male bill colour index, male body size index and female body size index, and measures of mate guarding and territorial defense behaviour over the Fert and Egg-fert stages for all attempts by each individual in each year

	Male bill colour	Male body size	Female body size
Mate Guarding			
Intra-pair distance (m)	0.019	0.029	-0.126
Male follows female	0.126	0.037	0.017
Male rendezvous	-0.049	-0.022	-0.421
Visual contact	0.049	0.231	-0.085
Territorial Defense			
Male perch height (m)	-0.153	0.118	0.159
Proportion time patrolling	-0.059	-0.418	-0.034
Boundary disputes /min.	0.176	-0.179	-0.251
N	15	17	16

After Bonferroni correction all $P>0.05$, 2-tailed.

garden, neighbouring males outside the study site were assigned a probability of being available based upon the average availability of all study males across the whole of that season. Over the Fert and Egg-fert stages for each breeding attempt TMP ranged from 0.44 to 0.96 (median 0.71, N=41). There was some suggestion of a decrease in intra-pair distance as TMP built up (Kendall correlation coefficient, intra-pair distance τ_{41}=-0.168, P=0.064), and also of an increase in the proportion of female moves followed by the male and in the proportion of rendezvous moves made by the male (male follows female τ_{41}=0.167, P=0.075, male rendezvous τ_{41}=-0.168, P=0.071), but these were not quite statistically significant. There were no increases the proprtion of time spent in visual contact nor in male territorial defence behaviour with increases in TMP (visual contact τ_{41}=-0.004, P=0.513 height τ_{41}=0.029, P=0.398, proportion of time spent patrolling τ_{41}= -0.112, P=0.836, rate of boundary displays τ_{41}=--0.170, P=0.924).

Discussion

Male blackbirds maintained closer proximity to their mate and followed more of her moves in the days leading up to and during egg laying. This corresponds to the females' presumed fertile period and is consistent with the mate guarding hypothesis (Birkhead & Møller 1992a; Birkhead 1998). There was no evidence in support of any of the alternative hypotheses for pair proximity (Birkhead & Møller 1992a, data not shown). The data suggest that males adjust their mate guarding effort to counter the increased risk of loss of paternity afforded by variation in female fertility (Birkhead 1998).

Male mate guarding behaviour may function to prevent females from engaging in EPCs, to prevent copulatory access to the female by other males, or both (Lifjeld et al 1994). The distinction between these two functional interpretations is important in terms of individual reproductive strategies and the sexual selection pressures they generate. The maintenance of intra-pair distance by male but not female blackbirds may reflect a conflict

of interest between the sexes over mate-guarding and suggests male-female competition (Lifjeld et al 1994). This is supported by the observation that females control the outcome of unforced EPC advances (Chapter Two) and suggests that extra-pair paternity arises out of female choice. Territorial defence however, is most likely to reflect male-male competition. It occurs in direct conflict to mate guarding behaviour since the male must leave the female to patrol the territory, to oust intruders and to engage in boundary displays with neighbours, yet it continues during the fertile stages of the females' reproductive cycle (Table 1). However, by preventing the access of other males to the territory, it serves to limit their access to the female and so may act as a secondary paternity guard.

Unlike some other passerine species, males did not remain on the ground within the "safe" 5m mate guarding distance (Davies 1985; Alatalo et al 1987; Møller 1987b; Birkhead & Møller 1992a); rather they habitually perched in a prominent position above the female. The tactic appears to offer the opportunity to combine scrutiny of the female's activities with monitoring of the territory for intruders. A similar pattern of behaviour is found in yellow warblers, *Dendroica petechia*, and in yellowhammers, *Emberiza citrinella*, defending exclusive territories in open habitat with good visibility (Hobson & Sealy 1989; Sunberg 1994). Dickinson & Leonard (1996) have also found that mate guarding distance increased with decreasing vegetation density in western bluebirds, *Sialia mexicana*, and it is likely that the tactic is a response to the visibility offered by open habitat.

The maintenance of territorial behaviour over the whole of the female's cycle (Table 1) suggests that it serves functions other than paternity protection. High perch heights may aid predator detection or allow the male to observe other females on neighbouring territories (Hobson & Sealy 1989). The maintenance of territorial boundaries may reflect the unpredictable re-mating opportunities afforded by the high rate of nest predation, by

ensuring that the male has a viable territory whenever his mate becomes fertile.

The intensity of mate guarding was greater in first year than in older males (Table 2) and this may reflect either the greater experience of older males or their greater average quality. If age reflects quality due to longevity (Manning 1985; Hansen & Price 1995; Kokko 1997; Møller & Ninni 1998), then older, higher quality males may suffer less risk of cuckoldry and adjust their mate guarding intensity accordingly (Gowaty & Bridges 1991; Kempenaers et al 1992; Kempenaers et al 1995; Lifjeld et al 1994; Johnson & Lifjeld 1995; Wagner et al 1996). Alternatively older, more experienced males may be more efficient in their paternity protection tactics and so can expend less effort on mate guarding. Møller (1985, 1987a, 1987b) suggests that this is reflected in a subtle shift in the trade-off between mate guarding and territory defence towards the latter in older and more experienced males. However, there were no differences in territory defence behaviour between the two age classes, suggesting that this is not the case (Table 2).

Two other potential measures of male quality did not reveal any relationship with the intensity of mate guarding or territorial defense. Sexual dimorphism in size and colouration are proposed to arise by sexual selection with larger size and brighter colouration reflecting higher quality (see Andersson 1994 and Møller & Ninni 1998 for reviews). Although there was some size dimorphism and individual variation in male orange/yellow bill colour that may reflect male quality (Bortolotti et al 1996), neither measure was related to variation in observed behaviour (Table 3).

There was some suggestion that mate guarding intensity varried with the proportion of males on the study site who were not mate guarding and so could potentially pursue EPCs more freely. Assuming that male guarding behaviour attempts to prevent the female from engaging in EPCs (see above), then such an increase in available males suggests an increase in opportunity for the females to copulate outside their pair-bond, and it may

follow that males showed a tendency to intensify their mate guarding behaviour accordingly (Møller 1985, 1987b; Meek et al 1994; Dickinson & Leonard 1997).

In summary, behavioural evidence indicates that male European blackbirds attempt to protect their paternity by mate guarding whilst also maintaining a high level of territorial defence. Mate guarding appears to limit opportunities for females to copulate outside the pair-bond, while territorial defense limits opportunities for extra-pair males to gain access to the pair female. Territorial defence remains constant throughout the reproductive cycle, but is combined with mate guarding by the male perching above the female. This appears to allow him to survey his territory and monitor the activities of his mate simultaneously. The intensity of mate guarding increases with peaks in female fertility and may increase with the availability of other males free to seek EPCs. It is more intense in first year males than older, which may reflect variation due to male quality. These data suggest that males vary their intensity of mate guarding with variations in female fertility and the risk of losing paternity to EPC males.

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Chapter Five: Female Mate Guarding: no evidence in a socially monogamous species

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To understand the behavioural aspects of sperm competition, the costs and benefits to both sexes should be considered. However few studies have addressed the costs to females of their social mate engaging in extrapair copulations (EPCs). Measures of female mate guarding have concentrated on female solicitation and copulation; however, females may also control access to their mate by maintaining close proximity, as is common in males. I recorded the maintenance of pair proximity behaviour of an urban population of the socially monogamous European blackbird, Turdus merula, *over three breeding seasons. There was no evidence that females guarded their mates to prevent them from engaging in EPCs, nor were there any effects of the potential quality indicators of age, body size or male bill colour on the intensity of mate guarding between individuals. The study adds to a small body of literature suggesting that female mate guarding may be found in (facultatively) polygynous species, but not in socially monogamous ones.*

Introduction

The extrapair copulation (EPC) strategies and counter-strategies of male birds have been widely studied (reviewed in Birkhead & Møller 1992; Birkhead 1998), but only more recently have the relatively subtle strategies of their mates received such focused attention (e.g. Smith 1988; Davies 1992; Sheldon 1994a; Gray 1997a, b). It is now widely accepted that females also actively pursue extrapair copulation strategies (e.g. Birkhead & Møller 1993; Gowaty 1996; Petrie & Kempenaers 1998), and it has been suggested that they may also use strategies to counter their mate's extrapair behaviour (Petrie 1992; Petrie & Hunter 1993).

These strategies invariably give rise to conflicts of interest between members of a mated pair, as each attempts to gain the benefits from their own extrapair copulatory activities, yet limit the costs incurred by the extrapair copulations of their mates. The benefits and costs to males are readily understood in terms of paternity success (Birkhead & Møller 1992), but those of females are rather more subtle (Hunter et al. 1993; Gray 1997a, b).

The female mate-guarding hypothesis (Petrie 1992; Petrie & Hunter 1993) suggests that female birds attempt to reduce the opportunity for their mate's infidelity by repeatedly engaging him in courtship and copulation. It is argued that this serves to decrease his opportunity and motivation for EPCs by using up his time, ejaculate reserves and sexual energy. This then reduces the chances that he will form pair bonds with other females and either switch mates or share his parental care (Birkhead & Møller 1992); it ensures that he has sufficient sperm to fertilize the female's own eggs (Sheldon 1994b); and it reduces the chances of his contacting and transmitting a sexually transmitted disease to her (Sheldon 1993). For females paired to high-quality males, the tactic may also prevent other females from having access to high-quality paternity for their offspring,

thereby avoiding the potential cost to the female's own offspring of having to compete with other high-quality individuals (Petrie 1994). Monogamously mated females, then, face the potential costs of losing their mate from mate switching or the costs of EPCs within the pair, whereas females in potentially polygynous partnerships face the cost of losing of paternal care to a secondary female as well as the costs of EPCs within the pair.

European blackbirds,*Turdus merula*, are socially monogamous, although extrapair courtship attempts by males are frequent (2.05 intrusions /h during the females' likely fertile periods) and may result in extrapair paternity (unpublished data). However, the frequency of observed copulations is very low and females do not appear to initiate copulations with either pair or extrapair males (Snow 1958; unpublished data). Paired birds associate closely throughout the breeding season, and although the male is primarily responsible for the maintenance of this proximity during the female's fertile period, females sometimes follow moves initiated by their mate, or join him when the two have been separated (unpublished data). Just as males use close proximity to guard females during their fertile period, so female blackbirds may be using proximity to guard against their mates seeking EPCs at other times.

For socially monogamous pairs, the female mate-guarding hypothesis predicts that females should guard their mates when there is a high risk of the male taking part in EPCs (Petrie 1992; Petrie & Hunter 1993). There is some suggestion that male blackbirds give priority to mate guarding over seeking EPCs from 5 days before egg laying begins until the day the penultimate egg is laid (unpublished data), indicating a higher risk of males seeking EPCs outside their mate's presumed fertile period. However, pair members are not always in visual contact (unpublished data), and the brief nature of courtship and copulation combined with high population density (3.4 territories /ha in this study), provide the opportunity for males to obtain

EPCs even when mate guarding. Although females in this study rarely left their territory and were never seen to initiate courtship, all observed pair and extrapair copulations were within the female's presumed fertile period (unpublished data), and the risk of the male achieving successful EPCs may depend upon the proportion of neighbouring females who were fertile at any one time.

The female mate-guarding hypothesis also predicts that females paired to high-quality males should guard more intensely, as such males are likely to be more attractive to other females as EPC partners. In addition, when there is a mismatch in partner quality, low-quality females paired to high-quality males should guard more intensely than females paired to males of matched quality, since such a male is more likely to seek to improve upon the quality of his mate (Petrie 1992; Petrie & Hunter 1993).

Male blackbirds are slightly larger than females and have a bright orange bill that varies in colour between individuals, and first-year and older birds can be distinguished by slight differences in plumage characteristics (Snow 1958). Sexual size dimorphism and dichromatism are frequently found to influence the degree of extrapair paternity within a nest (see Andersson 1994; Møller & Birkhead 1994; Møller & Ninni 1998 for reviews) suggesting that larger and more colourful birds are of higher quality and so are cuckolded less frequently because of female choice and/or male competition. Older birds who have survived longer may on average be of higher quality than first-year birds (Manning 1985; Hansen & Price 1995; Kokko 1997; Møller & Ninni 1998). Comparisons of behaviour between age groups and with variation in body size and male bill colour may be used to test these effects of mate quality predictions.

In this paper I explore female pair proximity behaviour as a female mate-guarding tactic in an urban population of European blackbirds and test the female mate-guarding hypothesis predictions that females guard more intensely when there is a high risk of their mate taking part in EPCs and that

females paired to high-quality males guard more intensely, especially when they are of low-quality themselves. I conclude with a comparative review of the literature on female mate guarding in monogamous and (facultatively) polygynous species.

Methods

I studied a colour ringed population of European blackbirds in Oxford Botanic Garden, UK (51°44'N,1°16'W), from 1991 to 1993 as part of a wider study on the birds' reproductive behaviour. I followed 16 male-female pairings, involving 12 males and 13 females. Each year between January and June I caught individuals in Potter traps (Davis 1981). The birds were aged and sexed by plumage characteristics (Snow 1958). I measured their wing and tarsus length (Spencer 1984; Yezerinac et al. 1992) and estimated by eye the percentage of the bill coloured yellow-orange and, from March 1991, the richest tone of this colour as matched in daylight to Pantone colour cards (Letraset™ by Pantone).

I calculated an index of body size for each bird in each year from principal components analysis of wing and tarsus length. The PC1 scores derived explained 72.0% of the variance with character loadings of 0.85 for both measures. T score transformation converted these into positive integers. I calculated an index of bill colour for each individual in each year using derivatives from the seasonal maximum of percentage of the bill coloured orange/yellow, multiplied by the rank of the colour from yellow to orange made by three naive observers from the 16 Pantone colour codes used in the study.

I observed nesting attempts from nest-building to fledging or until the attempt was lost, with the majority of observations concentrated on the days leading up to and including egg-laying. I collected data at all times during daylight hours, with a peak between 0600 and 1100 hours BST. Observations began when I located a focal pair on their territory and lasted

20 min or until the birds were lost from view for 2 consecutive min. Mean watch duration was 18.3 min, with an average of 5.5 watches per attempt and a total observation time of 67.41 h. I watched the birds from the periphery of their territory with no attempt at concealment, since they were habituated to human presence. The order in which the pairs were watched was random on each field day.

I recorded the association behaviour of the birds as (1) following of moves initiated by the partner, where the move was greater than 5m or out of perceived visual contact and the follow was made within 30 s; and (2) "rendezvous" moves, where an individual rejoined its mate after the pair had been separated for longer than one min and/or had been involved in independent activities. This was defined as moving to a position in direct visual contact and within 10m of its partner.

I collected data over 41 nesting attempts where the date of clutch initiation was known (37% first attempts, 39% second, 22% third and 2% fourth attempts). The date of clutch initiation and the final clutch size were determined from nest checks. Two nests were not found until after egg laying, and I estimated their date of clutch initiation from the day the chicks hatched, 13 days after the last egg was laid (Snow 1958). Fledgling success was low (27% across all years) and not all pairs succeeded in rearing young. Across all three seasons, only three further nesting attempts were made after a brood fledged sucessfully.

Most of data were not normally distributed and not readily amenable to transformation, so I used non-parametric statistical treatments unless otherwise stated. Where data were testing specific predictions of the female mate-guarding hypothesis, one-tailed probabilities were used. Rates of behaviour per min were derived from the duration of the watch and when combining data from several watches, I weighted averages by watch duration. The data were organized in relation to the day of the female's reproductive cycle, where day 0 indicates the day the first egg was laid. For

some analyses data are split into days with high risk and days with low risk of males taking part in EPCs. Low risk days are between days -5 and day +2 of the female's cycle, when the male is mate guarding (unpublished data). High risk days are all other days of the cycle.

Following Davies & Hatchwell (1992; Hatchwell & Davies 1992), I assume that the data for each breeding attempt are independent. Although six pairs contributed only one attempt, 10 contributed between two and seven (median 2.4) and may have introduced error from repeated sampling. However the variation in the intensity of female pair-association behaviour between different pairs was no greater than that within individual pairs over repeated attempts, indicating that the data were not biased by these repeated measures (unpublished data). Similarly, by including some individuals more than once when paired to different partners in different years, the data may be biased from repeated measures of the same individual. However conservative analyses that included each individual only once, show the same patterns of female pair-association behaviour as the full data set and indicate that the data were not biased by repeated measures of the same individual in different pairings (unpublished data).

Results

Risk of EPCs

There was no increase from days with low to days with high male EPC risk in the mean proportion of male-initiated moves followed by the female, in the mean rate of female rendezvous moves per min, nor in the mean proportion of all rendezvous within the pair that were initiated by the female (Wilcoxon signed-ranks, one-tailed: proportion of moves followed: Z=0.338, N=7 untied pairs, P=0.633; rate of rendezvous: Z=0.523, N=30 untied pairs, P=0.301; proportion of rendezvous: Z=0.971, N=20 untied pairs, P=0.834; Fig. 1). Neither were there any increases in these measures over all days with increases in the mean proportion of females on the study site who

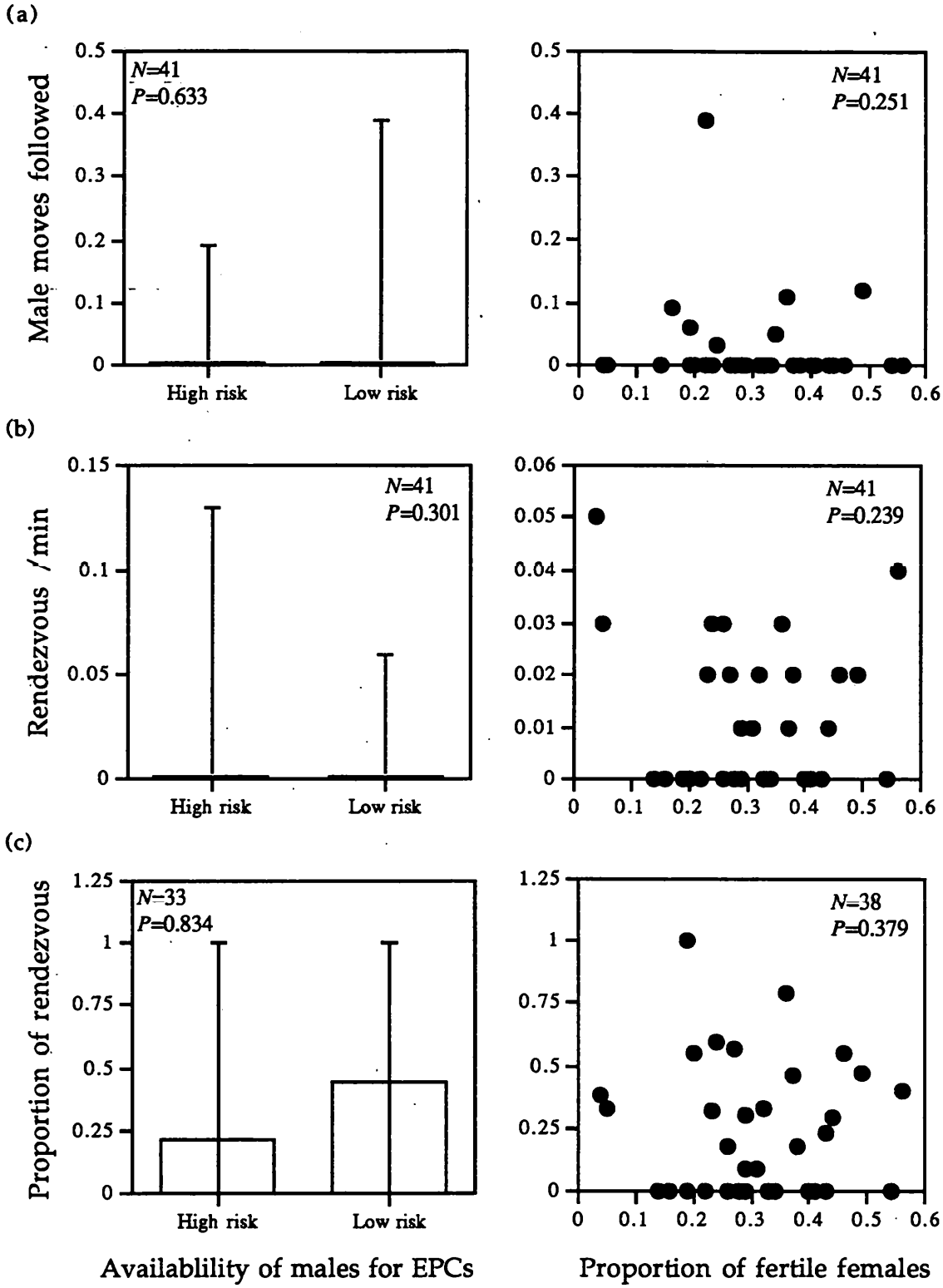

Figure 1. (a) The proportion of male-initiated moves followed by the female, (b) the rate of rendezvous moves initiated by females, and (c) where rendezvous moves were observed, the proportion of all rendezvous moves within a pair initiated by the female, in relation to male availability for seeking extrapair copulations (EPCs) and the proportion of fertile females available to accept them. Values are medians (+range), number of attempts. *P* values are on the figures, details of statistics are given in the text.

were being guarded by their mate and so were presumed to be fertile (Kendall's correlation coefficients, one-tailed: proportion of moves followed: τ=-0.085, N=41, P=0.251; rate of rendezvous: τ=-0.084, N=41, P=0.239; proportion of rendezvous: τ=-0.038, N=38, P=0.379; Fig. 1).

Effect of Mate Quality

There was no evidence of females paired to older males guarding any more intensely than females paired to first-year males, both over high-risk days and over all days of the attempt, when comparing mean pair association behaviour for all attempts by each female in each year (Table 1). Nor was there any evidence of first-year females guarding more intensely than older females (Table 1).

There was no increase in female pair association behaviour with increases in male body size, or decreases in female body size both over high-risk days and over all days of the attempt, when considering the mean for each female across all attempts in each year (Table 2). Nor was there any increase in measures of female mate guarding with increases in male bill colour both over high-risk days and over all days of the attempt, when considering the mean for each female across all attempts in each year (Table 2).

Two of the pairs of birds in the sample were first-year females paired to older males and three were both first-year birds. Three pairs were made up of smaller than average females paired to larger than average males, and in three pairs both male and female were below average in size. Although Mann-Whitney U tests (not shown) indicate no variation in female mate-guarding intensity with mismatches in the ages or sizes of the pairs, the power of statistical tests with such small sample sizes is very low and the null hypothesis is likely to be accepted in any case. However, from the data available (Table 3) there is no suggestion that low-quality (young or small) females paired to high-quality males guard more closely than those with low-quality mates, as is predicted by the female mate-guarding hypothesis.

Table 1. Summary of measures of female mate guarding by the age of her mate and by her own age, over high risk days for male extrapair copulations and over whole breeding attempts

	Mate's age				Female's age			
	1st year	Older	*U*	*P*	1st year	Older	*U*	*P*
Over high-risk days								
Male moves followed	0.00 (0.05)	0.00 (0.02)	23.0	0.443	0.00 (0.04)	0.00 (0.02)	31.5	0.338
Rendezvous/min	0.03 (0.03)	0.01 (0.02)	9.0	0.957	0.02 (0.03)	0.01 (0.03)	23.0	0.128
Proportion of rendezvous	0.64 (0.46)	0.16 (0.29)	5.00	0.982	0.54 (0.59)	0.18 (0.30)	17.0	0.062
N	3	16			5	14		
Over whole attempt								
Male moves followed	0.00 (0.03)	0.00 (0.04)	26.0	0.449	0.00 (0.04)	0.00 (0.05)	38.0	0.582
Rendezvous/min	0.02 (0.02)	0.01 (0.02)	13.0	0.924	0.02 (0.02)	0.01 (0.02)	29.0	0.177
Proportion rendezvous	0.45 (0.44)	0.14 (0.35)	12.0	0.926	0.45 (0.50)	0.14 (0.29)	23.5	0.110
N	3	18			5	16		

Data are medians (IQR) for all attempts by each individual in each year, *N* is the number of individuals, statistics are Mann-Whitney *U* tests, *P*-values are one-tailed.

Table 2. Kendall's correlation coefficients between the mean measures of female mate guarding for all attempts by each individual in each year, and male body size index, female body size index and male bill colour index, over high risk days for male extrapair copulations and over whole breeding attempts

	Male body size	Female body size	Male bill colour
Over high risk days			
Male moves followed	0.055	-0.126	-0.070
Rendezvous/min	-0.453	0.000	0.042
Proportion of rendezvous	-0.384	0.252	0.000
N	15	15	13
Over whole attempts			
Male moves followed	0.267	-0.162	0.025
Rendezvous/min	-0.344	0.009	0.134
Proportion of rendezvous	-0.276	0.177	0.175
N	17	16	15

N is the number of individuals, one-tailed $P>0.05$ for all measures

Table 3. Summary of measures of female mate guarding by the relative ages of the members of a pair and by their relative body sizes, over high risk days for male extrapair copulations and over whole breeding attempts

	Ages of pair			Body sizes of pair			
	Both 1st year	Male older	Both older	Both small	Male large	Both large	Female large
Over High Risk Days							
Male moves followed	0.00 (0.05)	0.01 (0.03)	0.00 (0.02)	0.00 (0.04)	0.00 (0.08)	0.00 (0.00)	0.00 (0.19)
Rendezvous/min	0.03 (0.03)	0.01 (0.02)	0.00 (0.01)	0.02 (0.03)	0.00 (0.00)	0.00 (0.01)	0.03 (0.03)
Proportion of rendezvous	0.64 (0.46)	0.27 (0.54)	0.16 (0.30)	0.19 (0.63)	0.00 (0.02)	0.08 (0.16)	0.63 (0.62)
N	3	2	14	3	3	3	4
Over Whole Attempts							
Male moves followed	0.00 (0.03)	0.02 (0.04)	0.00 (0.05)	0.00 (0.03)	0.04 (0.18)	0.00 (0.00)	0.00 (0.08)
Rendezvous/min	0.02 (0.02)	0.01 (0.01)	0.01 (0.02)	0.00 (0.03)	0.00 (0.01)	0.00 (0.01)	0.02 (0.02)
Proportion rendezvous	0.45 (0.44)	0.27 (0.54)	0.14 (0.29)	0.06 (0.58)	0.02 (0.15)	0.70 (0.14)	0.29 (0.51)
N	3	2	16	3	3	3	4

Data are medians (IQR) for all attempts by each individual in each year, *N* is the number of individuals across all three years.

Table 4. Available estimates of extrapair paternity in the populations of monogamously mated species where female mate guarding has been investigated

	Rate of extra-pair paternity (%)		
Species	Nestlings	Nests	Source
Crested tit	12.4 (15/121)	30 (6/20)	Lens et al. 1997
Willow tit	0.89	4.2	Orell et al. 1997
American kestrel	11.2 (10/89)	9.5 (2/21)	Villarroel et al. 1998
European blackbird	14 (2/14)	29 (2/7)	E.Creighton, unpublished data

Discussion

There was no evidence of female mate guarding by close association in this population of European blackbirds. Females did not increase their pair association behaviour with potential increases in the risk of males engaging in EPCs, nor were there any effects of potential differences in the quality of individuals as measured by age, body size or male bill colour. Female European blackbirds do not appear to guard their mates as predicted by the female mate-guarding hypothesis (Petrie 1992; Petrie & Hunter 1993).

This study adds to a small but illuminating number of papers addressing the female mate-guarding hypothesis. Evidence in support of the hypothesis that females repeatedly court and copulate with their mates as a form of mate guarding is found in (facultatively) polygynous species, including the blue peafowl, *Parvus cristatus* (Petrie et al. 1992), the European starling, *Sturnus vulgarus* (Eens & Pinxten 1995) and the blue tit *Parus caeruleus* (Kempenaers et al. 1995); and is likely in the tree swallow, *Tachycineta bicolor* (see Whittingham et al. 1994, 1995; Eens et al. 1995). The observations that resident female red-winged blackbirds, *Agelaius phoeniceus*, solicit copulations from their mate when new females arrive on the territory (Hurly & Robertson 1984), and that female blue tits mated to high-quality males follow more of their moves than those mated to low-quality males (Kempenaers et al. 1995) add further support.

However, in socially monogamous species no evidence of female mate guarding has been reported to date. In the razorbill, *Alca torda* (Wagner 1996), the crested tit, *Parus cristatus* (Lens et al. 1997), the willow tit, *Parus montanus* (Welling et al. 1997), and the American kestrel, *Falco sparverius* (Villarroel et al. 1998), the authors concluded that observed female solicitation outside their fertile period serves purposes other than to guard their mates. This is despite evidence of EPC behaviour in all these populations and estimates of extrapair paternity in most (Table 4; no

paternity data are vailable for razorbills). It appears that the potential cost of male EPC behaviour to these females is not sufficiently high to have selected for female mate guarding. This paper adds to this list no evidence for female mate guarding in the socially monogamous European blackbird, using a test for a more subtle form of mate guarding by close proximity.

Although these studies of female mate guarding are few, they suggest that whilst females of polygynous species may guard their mates, females of socially monogamous species apparently do not. If these findings are borne out by further studies of female mate guarding, either repeated courtship and copulation or pair proximity, then the implications for the hypothesized costs to females of male infidelity may be important.

The female mate-guarding hypothesis argues that monogamously mated females face the cost of losing their mate to another female (mate switching), or the costs of EPCs within the pair, including the depletion of sperm reserves, the transfer of sexually transmitted diseases and increased competition from the extrapair offspring of high-quality males (Petrie 1992; Petrie & Hunter 1993). However, studies of mate switching in species with monogamous breeding patterns suggest that it is rare once breeding pairs have formed (Birkhead & Møller 1992) and the risk of this cost is likely to be very low. The review of studies presented above suggests that the remaining potential costs of EPCs are not sufficiently high to promote mate guarding by monogamously mated females, at least in the populations reported here.

Polygynously mated females, on the other hand, do appear to face the real cost of reduced parental care when their mate attracts additional females (reviewed in Slagsvold & Lifjeld 1994). The finding of mate guarding by females in (facultatively) polygynous species suggests that these costs do appear to be sufficiently high to drive selection for female mate-guarding behaviour.

Overall, the literature to date indicates that female mate guarding may be relevant only to females in polygynous breeding patterns. However,

both frequent copulation and male mate guarding by close association are known to be costly in terms of time and energy (Birkhead & Møller 1992; Westneat 1994; Birkhead 1998), and this is also likely to be true for females. Monogamously mated females may attempt to counter the lower costs of their mates' EPC strategies by using less costly methods, for example by limiting their strategy to direct aggression targeted at potential EPC females (Slagsvold & Lifjeld 1994; Whittingham et al. 1995; Villarroel et al. 1998).

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Chapter Six: Mate acquisition in the European blackbird and its implications for sexual strategies

The social constraint theory of sperm competition predicts that females who are constrained in their choice of social mate at mate acquisition may improve upon the quality of their genetic mate by engaging in mixed reproductive strategies during the breeding season. Female European blackbirds, Turdus merula, *have been shown to engage in mixed reproductive strategies and here I investigate if and how these females are constrained in their choice of social mate. I recorded patterns of territorial distribution and interactions between resident birds both before and during the breeding season. Patterns of observed behaviour agreed with earlier descriptions of winter and breeding territoriality and provided clues to the underlying mechanism of mate acquisition. I conclude that the constraint on breeding success imposed by high nest predation promotes intra-sexual competition for nesting habitat between females prior to pair formation. Female distribution promotes intra-sexual competition between males for territorial area overlapping females or for habitat likely to be occupied by females. Mate choice during pair formation is severely constrained by the outcome of this intra-sexual competition and typically overlapping territorial males and females pair into social monogamy on a shared breeding territory. The data support the social constraint theory of sperm competition as an explanation for mixed reproductive strategies by female European blackbirds.*

Introduction

The constrained female choice hypothesis predicts that females engaging in mixed reproductive strategies are making "the best of a bad job" (Trivers 1972, Dawkins 1976) when ecological or social constraint has limited their choice of social mate (Møller 1992, Gowaty 1996), and they may improve upon the genetic fitness of their off-spring by mating with superior males outside of their social bond (Mulder et al 1994, Hasselquist et al 1996, Kempenaers et al 1997, Sheldon et al 1997). So, both the process of mate acquisition and the subsequent reproductive strategies adopted in the breeding season contribute to the sexual selection pressures acting upon individuals (Møller 1994a, 1998).

European blackbirds have been found to engage in mixed reproductive strategies leading to extra-pair paternity, and there is little evidence that females gain anything other than genetic benefit from extra-pair copulations (Chapter Three). This strategy may reflect females' attempts to improve upon the quality of their genetic mate when they have been constrained in their choice of social mate. In this paper I explore the mate acquisition process in the Oxford Botanic Garden population of European blackbirds to determine the nature of the constraints acting upon female choice of social mate and the implications this may have for sexual selection in this species.

Behaviour associated with pair formation in blackbirds has been described in the literature by several authors, but little evidence for the process of mate acquisition has been discussed. Descriptions of excited gatherings of displaying and/or fighting (usually male) blackbirds in late winter and early spring have been reported (Morley 1937, Lack 1941, Lack & Light 1941), and have been suggested to serve a function in mate acquisition (Morley 1937). More detailed work (Jackson 1954, Snow 1956, 1958, Lack 1966, Edwards 1983) however, suggested that mated pairs develop from "apparent

pairs" of resident males and females whose winter territories overlap (Snow 1956, 1958). Apparent pairs changed throughout the winter as females moved territories or the mosaic of male territories shifted due to the insertion of a new male territory, though previously mated birds tended to stay on the territories they defended during the previous breeding season. However, beyond the observation that a territory was a prerequisite for breeding in both sexes and an implicit assumption that females joined males on their territories (Snow 1956, 1958), the actual process of mate acquisition has not been addressed.

Studies of mate acquisition in other territorial species suggest a number of different patterns are found. Where pairs form from mate choice during communal displays over winter, then already mated pairs may settle together (eg Williams 1983, Sorenson 1992, 1994). However, in migratory species males typically arrive on the breeding site before the females, with the highest quality males arriving first to claim the best quality habitat (Møller 1994a, 1994b, Kokko 1999) and the females arriving a few days later (presumably also competitively) to choose between (competitive mate choice, Altman et al 1977, Halliday 1983). Though whether female choose on the basis of characteristics of the male (eg Catchpole 1980, Lifjeld & Slagsvold 1988, Hasselquist et al 1996, Mountjoy & Lemon 1996), or on the basis of his territory (eg Gottlander 1987, Radesäter et al 1987) is difficult to determine, due to the inevitable correlation between the qualities of males and the resources they defend (Davies 1978, Searcy 1982).

In more resident species mate acquisition has been found to arise as a consequence of over-lapping territorial males and females forming social bonds at the start of the breeding season (Davies 1992). Here females are proposed to settle in competition with each other for suitable breeding habitat and independently of the territorial patterns of males (independent female settlement). Males are proposed to impose themselves on the female distribution and compete to monopolise female territories.

Methods

Behavioural observations

I studied the territorial behaviour of a colour ringed population of European blackbirds in in Oxford Botanic Garden, UK (51°44'N,1°16'W) from January to June 1993 as part of a wider study of the birds' reproductive behaviour.

From January to mid-March I made daily systematic searches of the study site, usually in the morning when territorial activity is at its highest (Edwards 1983). The search route ensured all areas were equally covered, taking into account the topographical features and vegetation structure of the garden. I recorded on a map of the site the identity and first observed position of each territorial bird, identified by their dominant behaviour over non-territory holders and intruders, including assertive body postures, beak wipes, flight displays, boundary displays with territorial neighbours, chasing intruders, and fights (Snow 1958). I recorded subsequent positions and the sex and identity of opponents if the bird moved more than five metres or engaged in territorial interactions with conspecifics. Disputes at territorial boundaries were recorded as three positions corresponding to the extremities and mid-point of a boundary display, or the area over which a fight took place.

During the breeding season I recorded the positions of territorial birds during 20 minute focal watches of breeding pairs and during infrequent systematic searches of the garden as described above.

The positional data were transcribed into six figure grid references for analysis using the radio tracking data analysis programme *Wildtrack* (Todd 1993).

Removal experiment

In January and February I trapped known territorial but unpaired individuals and removed them from their territory for three days, a period

within which blackbirds react to natural territorial vacancies (Snow 1958, pers obs). The removed birds were held in a well-ventilated and undisturbed shed near the study site, in cages measuring 100cm x 50cm x 50cm, and fed *ad lib* with soft bill bird food, fresh fruit and water.

I collated territorial patterns for the three days before, during and after the removal to assess the effect of removal on the territorial distribution of the birds that remained. For this assessment, any bird seen exhibiting overtly dominant behaviour in the experimental area for a minimum of half a day in each of the three day stages of a trial was regarded as territorial for that stage.

Statistical methods

The positional data I collected for each bird were essentially independent fixes, weighted by a factor of three towards territorial boundary disputes (three positions corresponding to the extremities and mid-point of a boundary display, or the area over which a fight took place). The temporal separation between initial fixes of the birds' positions - a minimum of 2hrs up to a maximum of several days - ensured their independence (Swaihart & Slade 1985a). The inclusion of fixes after a move greater than five metres or on engaging in a territorial interaction added a source of temporal autocorrelation to the data set (Swaihart & Slade 1985b), but this has been demonstrated to have no effect on the nonparametric minimum convex polygon technique that I used here (Andersen & Rongstad 1989).

I used minimum convex polygons as a simple but effective method of determining territory outlines from positional data that included indications of boundaries (Kenward 1987). As a non-parametric technique it is unaffected by mild autocorrelation in the data (see above) and is robust when the number of data points are low (Harris et al 1990). Unless otherwise stated, I included only boundary outlines with sufficient points to provide a stable estimate of territory area - indicated by the plot of number of fixes

against enclosed area reaching a stable plateau (Kenward 1987). For direct comparisons of overlapping territory areas, I used equal numbers of data points for each territory to avoid any possible confounding effects due to correlations between the number of data points and territory area.

The different methods of data collection I used before and after pairing prevented direct comparisons of rates of behaviour and I have restricted the analyses to frequencies of individuals observed expressing the behaviour during specified periods of the study. These analyses included all territorial birds in the study site, including those whose territories were not included in the territorial analysis due to restricted observational access (eg territories extending onto private land at the edges of the study site).

Vegetation cover

In February, I plotted the vegetation structure of the garden onto a map of the study site by indicating the areas of lawns and flowerbeds, paths and buildings and shrubbery and climbing plants. Although a great deal of information was lost by plotting three dimensional structures onto a two dimensional map, the percentage of the overlaid territory areas that included such vegetation structures provided an index of the habitat type occupied by the birds' territories.

Results

Pairing dates

The process of pair formation in blackbirds takes place over several days (Snow 1958). Prior to pair formation, the two sexes generally ignore each other, though males will aggressively chase females when the two meet. During pair formation male behaviour towards females switches from aggression to courtship, to which pairing females become increasingly receptive and copulations may occur. Once paired the birds associate

together on their territory with the female dominant over the male (Snow 1956, 1958, Lack 1966, Chapter Three).

Six of the eight breeding pairs formed in the last week in February, one in the first week in March and one at the end of the first week in April. Accordingly, I collated data over the six weeks from the 10th January to the end of February as pre-pairing data and over six weeks from the 7th April until the 24th May for comparison as breeding data. Prior to pairing, all interactions I observed between overlapping birds involved the male directing aggression towards the female (6/10 resident males) whilst after pair formation all instances of aggression I observed between paired birds was directed at the male by the female (5/10 breeding females).

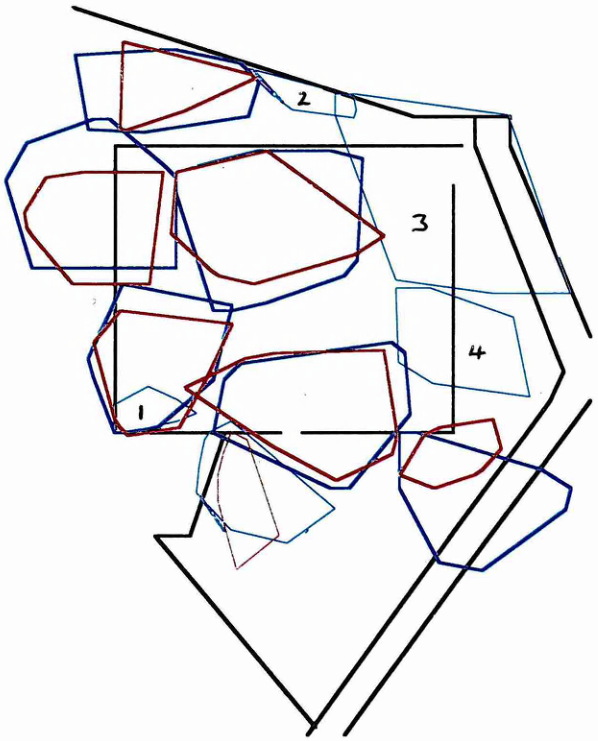
Territorial distributions

Prior to pair formation both sexes defended exclusive winter territories within their sex with overlap between the territories of males and females (Figure 1). All of the female territories were overlapped by males but not all of the male territories overlapped by females. After correction to an equal number of data points for each pair-wise comparison there was no difference in the areas of overlapping male and female territories and the majority of their statistical centres lay within 10m of each other (median=4.8m, range=3.2-19.3m) (Table 1).

Like the winter territories, breeding territories were exclusive within each sex and the territories of overlapping males and females were congruent (Figure 2). All females occupied a breeding territory with a male, but one male remained unpaired throughout the breeding season. After correction to the same number of data points for each pair-wise comparison, overlapping males and females occupied similar areas and all of their statistical territory centres lay within 10m of each other (median=6.8m, range=3.2-10.1m) (Table 1).

There was no difference in the before and after pairing distances between the centres of overlapping male and female territories (Table 1).

Figure 1. Overlap of male (blue) and female (red) territory outlines prior to pair formation. Outlines are shown for the last resident bird in the area, fine outlines indicate insufficient fixes to give a good estimate of territory outline or territories with boundaries outside the study site.



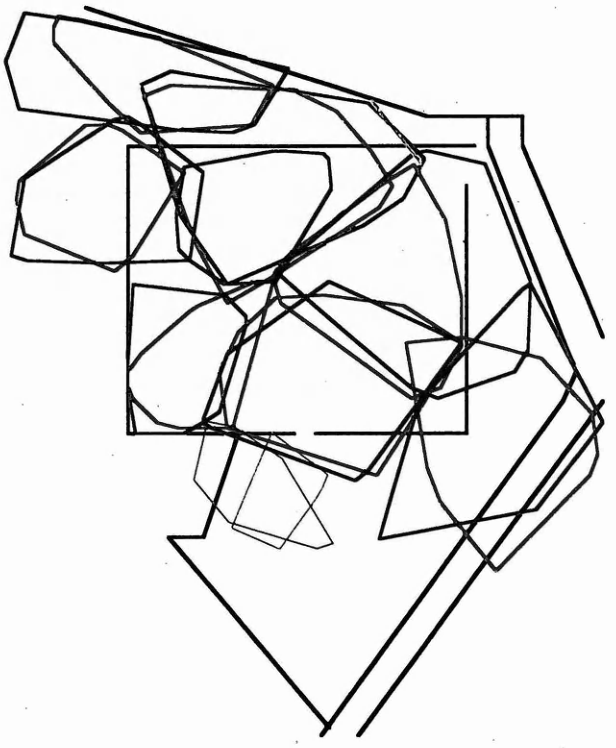
1. floater male failed to force a new territory between existing male territories,
2. male remained unpaired, but gained ground to the south when the neigbouring male damage his foot,
3. male abandoned this territory at pair formation to join an unpaired female outside the study site,
4. male moved north when the above male abandoned his territory, but then returned to this area when an unpaired female settled.

Table 1. Territorial areas of overlapping males and females after correction to equal numbers of data points for each pair-wise comparison, and the distances between their statistical centres

Before pairing				Breeding season			
Area (m^2)[1]				Area (m^2)[2]			
Males	Females	Centres dist (m)	No. fixes	Males	Females	Centre dist (m)	No. fixes
2756	2418	3.2	65	4099	4079	9.0	85
1577	1597	3.2	64	1910	1782	3.2	46
2336	1759	4.5	42	2181	2144	6.4	55
1185	884	5.1	30	2998	193	3.6	31
1889	2458	14.4	46	1533	4495	6.8	44
1331	604	19.3	29	4168	3912	10.1	46
				5437	3671	9.8	111

1. Difference in areas of overlapping pre-pairing territories, Wilcoxon signed ranks test, $Z_6=5$, $P=0.313$,
2. Difference in areas of overlapping breeding territories,Wilcoxon signed ranks test, $Z_7=7$, $P=0.296$,
3. Difference in the distances between centres of overlapping territories before and after pairing, Mann-Whitney U test, $U_{6,7}=40$, $P=0.418$.

Figure 2. Overlap of male (blue) and female (red) territory outlines during the breeding season. Fine outlines indicate territories with boundaries outside the study site. The green outline indicates the territory of the unpaired male who persistently intruded into the neighbouring territory to the south where the resident male had damaged his foot.



Effect of vegetation structure

Female winter territories were not evenly distributed over the study site (Figure 1). The occupied areas contained a higher proportion of lawns and flowerbeds, over three times the proportion of shrubbery and climbers, but a lower proportion of buildings and pathways than found in the unoccupied areas (Table 2). Male winter territories, however, occupied all parts of the study site including the areas not favoured by females (Figure 1).

Male-male territorial interactions

On winter territories I observed territorial males ousting intruders of both sexes, but during the breeding season I observed them oust mainly other males (Table 3). Territory boundary disputes were observed only with other males both before and after pairing, though during the breeding season males were sometimes accompanied by their mate when engaging in boundary disputes with neighbouring pairs (Table 4)

This boundary display analysis assumed that each combination of neighbours generated statistically independent data, even though individuals were included more than once when interacting with different neighbours. However, conservative analyses using each individual only once show similar results to the full analysis and indicate that the data were not biased by repeated measures (G-test with Williams correction (Sokal & Rohlf 1995); before pairing, G_2=10.17, P< 0.01; after pairing, G_2=5.484, P>0.05).

Female-female territorial interactions

On both winter and breeding territories I observed resident females oust only female intruders (Table 3). I never observed females on winter territories engage in boundary displays with their neighbours (Table 4). However, during the breeding season females were just as likely to be observed in boundary displays with neighbouring birds as their mates, though displays with neighbouring males only occurred when the female cooperated with her mate in a joint defence of their territory boundary (Table 4).

Table 2. Habitat type of areas of the study site occupied and unoccupied by female winter territories, X^2=53.9, *df*=2, *P*<0.001

	Area of habitat type (m^2)		
	Lawns & flowerbeds	Shrubs & climbers	Buildings, paths & ponds
occupied	13695 (68%)	680 (10%)	1420 (22%)
unoccupied	3660 (51%)	220 (3%)	3260 (46%)

Table 3. Territorial birds seen ousting intruding birds only of the same sex, only of the opposite sex and of both sexes, before pairing and during the breeding season. Statistics are G-tests, *df*=2

	Sex of ousted individuals				
	Only same sex	Only opposite sex	Both sexes	*G*	*P*
Before pairing[1]					
Males	5 (42%)	1 (8%)	3 (25%)	2.7	>0.200
Females	3 (38%)	0	0	5.4	<0.050
Breeding season					
Males	6 (60%)	0	2 (20%)	7.7	<0.050
Females	4 (44%)	0	0	7.6	<0.050

Table 4. The observed occurrence of boundary displays between neighbouring birds before and after pair formation. Statistics are Chi Squared tests, $df=2$

	Observed territory boundary interactions between neighbouring birds				
	Male-male	Female-female	Male-female	X^2	P
Before pairing[1]					
observed interactions	14 (67%)	0	0	25.4	<0.001
all possible interactions	21	11	26		
Breeding season					
observed interactions	11 (58%)	8 (62%)	10 (30%)[2]	3.1	>0.100
all possible interactions	19	13	33		

1. Overlapping males and females were not observed to co-operate in joint boundary displays,

2. All male-female interactions took place during interactions between pairs.

Territorial replacements and movements

Due to the difficulty in trapping previously handled birds I caught only four ringed territorial individuals for experimental removal prior to pair formation. In three trials involving the removal of a female, the overlapping pattern of male territories did not change and the experimentally removed females were replaced by floaters. On release, two of the three experimental females regained their territory, actively displacing the replacement female who rejoined the floater population.

Two cases of natural replacement of females was observed. Although no active competition was observed between the new and old residents, there was no evidence of either territory being abandoned by the original owners prior to the arrival of the replacement. Both displaced owners were later seen in the floater population.

In the single male-removal trial the vacancy was not filled, nor did the overlapping female move and I did not observe her in any other areas of the garden during the male's removal. This was in contrast to observations of natural replacements of males where floater males were frequently observed to challenge the territorial boundaries of established males. One male succeeded in defending a small territory between two established territories over three weeks in late January and early February, but despite almost continuous challenging of his neighbours boundaries, he did not succeed in forcing a new territory between them.

I observed further natural territorial movements during pair formation. Six breeding pairs formed between six of the resident winter males and overlapping females. A seventh formed between a resident male and a new female who replaced the winter resident female. The eighth was formed late in the season when a female from the floating population tried and failed to establish herself on the southern edge of the study territories, before moving to the area that had been abandoned by one of the unpaired

males five weeks earlier. Immediately on her arrival the nearby unmated male moved his territory to overlie hers and the two paired.

Two of the remaining winter male residents abandoned their territories. One disappeared from the study area and the other moved out of the study site to join an unmated female across the river. One of the abandoned territories was annexed by a neighbouring male, and the other remained vacant until the arrival of the eighth female (described above). The final male remained unpaired on his winter territory throughout the breeding season, but persistently intruded into a neighbouring territory who's resident male had a damaged foot. The damaged foot prevented this male from defending his full winter territory into the breeding season and he lost ground to the neighbouring unpaired male. The resident female continued to roam over the whole of the territory she had defended during the winter, coming to overlap both males. However, she built all her nests in a dense thorny tree in the damaged foot mate's territory and only he was seen to provision the nestlings from the clutch that hatched.

Discussion

Prior to pair formation both males and female blackbirds defended exclusive within-sex late winter territories and, as Snow (1956, 1958) and Edwards (1983) found, the majority of breeding pairs were formed between overlapping territory holders. There was no evidence of already mated pairs settling on a territory together, refuting suggestions made in the early literature that blackbirds pair during late-winter gatherings of displaying and fighting birds (Morely 1937, Lack 1941, Lack & Light 1941).

As reported by Snow (1956, 1958) males defended their late winter territories against intruders of both sexes, including directing aggression at the overlapping female, and they engaged in often protracted boundary disputes with their male neighbours. This behaviour suggests that males were in competition with each other for a territorial area, as illustrated by

accounts of males attempting to insert new territories between those of established males by challenging and forcing back the territorial boundaries (Snow 1956, 1958, Edwards 1983).

In contrast to males, and again in agreement with Snow (1956, 1958), females were not observed to engage in boundary disputes on their late winter territories but did aggressively chase away any female intruders. Combined with the observations of experimentally removed females regaining their territories from replacements and of natural territorial replacements (Snow 1956, 1958), this behaviour suggests that females were in competition with each other for resources, but that these resources did not depend upon territorial area *per se*.

Female late winter territories were confined to areas of the garden with higher proportions of shrubbery and climbers. A review of the breeding ecology of European blackbirds has shown the central importance to territory dispersion and reproductive success of dense nesting cover and alternative sites for repeat nesting attempts after predation (Chapter Two). Females defending winter territories in areas of dense vegetation appear to have been defending future nesting resources.

This was unlikely to be true for males since nesting cover was clumped and did not therefore depend upon territory area. Whilst foraging resources may have been related to territory area, the birds collected much of the food for nestlings and fledglings from nearby playing fields (Snow 1956, 1958, Edwards 1983, pers obs) and food availability on the territory has been found to have little effect upon breeding success (Edwards 1983).

It is not immediately obvious whether the congruency of over-lapping male and female late winter territories was due to females competing to settle within an area defended by a single male (competitive mate choice) as earlier work assumes (Snow 1956, 1958), or whether males were competing to defend an area occupied by a settled female (independent female settlement). However, two observations of territorial movements by

males to join already settled females during pair formation suggest independent female settlement. Similarly the independence of female territories is suggested by the observation that the female paired to the male with the damaged foot continued to use the full extent of her territory even when her mate was pushed into a smaller area by the neighbouring unpaired male (Figure 2). Snow (1958) adds further support with one report of an unmated male moving to pair with an already settled female and two cases of apparent polygyny where two exclusive female territories came to lie within an area defended by a single male in a pattern reminiscent of polygyny arising out of independent female settlement in dunnocks, *Prunella modularis* (Davies 1992).

In either case, mate acquisition in urban European blackbirds arises from the outcome of competitive settlement of females on late winter territories offering high quality nesting habitat and the competitive settlement of males on late winter territories either overlapping female territories or in areas where females might settle. Breeding pairs form between overlapping territorial males and females between late January and early March. As a result there is little scope for mate choice by either sex due to the constraints imposed by competition from members of the same sex and the sexual selection pressures operating during mate acquisition will be heavily biased towards intra-sexual competition.

The largely resident nature of the birds provides ample opportunity for competition within each sex and the highest quality individuals would be expected to gain ownership of the highest quality territories (Davies 1978, Searcy 1982). There is some evidence to support this hypothesis from changes of territorial ownership in this and other urban populations (Edwards 1983, Desrochers & Magrath 1993, Chapter Two) suggesting a tendency towards assortative mating by competitive ability. However, lower quality females paired to lower quality males may be able to improve upon

the quality of their genetic mate by engaging in extra-pair copulations with higher quality males during the breeding season (Møller 1992, Gowaty 1996).

This is supported to some extent here by the observed changes in patterns of territorial interactions before and after pair formation. As Snow (1956, 1958) also found, males continued to aggressively defend their territory boundaries against their male neighbours, but they ceased to direct aggression at female intruders during the breeding season and I have shown elsewhere that males will engage in courtship or attempted copulation with extra-pair females whenever the opportunity arises (Chapter Three).

Females continued to aggressively oust only female territorial intruders, but in contrast to their pre-pairing behaviour, began to engage in territorial boundary disputes with their female neighbours during the breeding season (Snow 1956, 1958). This suggests a shift in emphasis to defense of territorial area, though as discussed above this is unlikely to reflect a defense of material breeding resources. In other species female defense of territory area has been interpreted as a strategy to prevent polygyny or mate switching and the accompanying loss of paternal care and so female reproductive success, by preventing other females from forming social bonds with the resident male (Arces 1989, Dunn & Hannon 1991, Davies 1992, Slagsvold & Lifjeld 1994). I have shown elsewhere (Creighton 2000 - Chapter Five) that in contrast to males (Chapter Four) females do not actively guard their mate against taking part in EPCs, but they may be using defense of territorial area during the breeding season to prevent polygyny and limit the reproductive strategies of their mates to social monogamy and extra-pair copulations (Creighton 2000 - Chapter Five).

In conclusion, both sexes are constrained in their choice of social mate by intra-sexual competition for late winter territories leading to the formation of social pairs between overlapping territorial males and females. However, females may improve upon the quality of their genetic mate by engaging in extra-pair copulations with males of their choice after pair

formation (Creighton 2000 - Chapter Five). Males may improve upon their reproductive success by seeking EPCs with neighbouring females (Creighton 2000 - Chapter Five), but female territorial defense during the breeding season appears to limit their opportunity for polygyny. These data support the hypothesis that constraint in the choice of social mate during pair formation may drive female extra-pair sexual strategies during the breeding season.

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Chapter Seven: Concluding comments

In the Introduction to this thesis I outlined the four aims of the thesis as (1) to test current theory on the costs and benefits driving reproductive strategies in birds by (2) exploring in detail the reproductive strategies of individuals within one population, (3) determining how conflicts of interest between individuals are resolved, and (4) exploring the influence of ecological and social conditions on the behavioural traits expressed. Here I consider how these aims were met and what contribution this thesis makes to our knowledge of European blackbirds, to the theoretical and empirical knowledge in behavioural ecology and to knowledge in avian research in general. For clarity I consider aims two to four first. Finally I conclude with a brief outline of the implications of this thesis for future research.

Outcomes of the Thesis

The reproductive strategies of European blackbirds

Previous work on European blackbirds has provided a sound knowledge of the birds breeding biology (reviewed in Chapters One, Two and Six) and in this thesis I add new knowledge of the mate acquisition and reproductive strategies that give rise to this biology. In Chapter Six I establish that mate acquisition arises out of intra-sexual competition over breeding resources. In Chapter Three I show that both male and female European blackbirds engage in mixed reproductive strategies. Males seek extra-pair copulations (EPCs) by intruding onto the territories of their neighbours to court the resident female, or when several males intruded

simultaneously, to attempt to force copulations upon her. Females appear only to accept or reject these advances, though they may create opportunities to be approached by moving away from their mate during their fertile periods.

The conflicts of interest between individuals

Mixed reproductive strategies by both males and females create conflicts of interest between members of a mated pair as each attempts to increase their reproductive success whilst they reduce the costs associated with the extra-pair copulation strategies of their mate (Birkhead & Møller 1992). In Chapter Four I show how males attempt to thwart the EPC behaviour of their mates by keeping in close association with the female during her presumed fertile period. In Chapter Five I contribute a new test of how females may counter their mate's EPC strategies, but establish that females did not guard their mates either by repeated copulation or by close association.

Male EPC strategies also create conflicts between males as each attempts to increase their own reproductive success at the expense of another male's parental effort (Trivers 1972). In Chapter Four I show how males attempt to prevent other males from gaining sexual access to their mate by vigorous defense of their territory. Though as I describe in Chapter Three, intruding males can enter neighbours' territories with great stealth and often succeed in approaching the female undetected; or when several intrude simultaneously they can overwhelm the resident male and apparently force copulations upon the female.

Female EPC strategies may also create intra-sexual conflicts of interest (Petrie 1992; Petrie & Hunter 1993). However the lack of overt female extra-pair sexual tactics (Chapter Three) offered little suggestion for female-female conflict, though the territorial interactions between females reported in Chapter Six may indicate that females engaged in territorial defense to prevent other females from forming social bonds with their mates.

The influence of social and ecological conditions

Throughout this thesis I have considered how the birds' reproductive strategies are influenced by the prevailing ecology and social environment and have attempted to explain the effects these have on both the birds' reproductive strategies and the tactics used by individuals in their sexual endeavours.

Chapter Two identifies the central importance of nesting cover on the rate of nest predation and so reproductive success. Chapter Six pin-points the role of nesting cover in determining the pattern of mate acquisition and explains how this constrains females' choice of social mate, leading to female mixed reproductive strategies during the breeding season. However, the tactics used by females to improve upon the genetic quality of their mate appear to be constrained by the social environment, whereby overt sexual behaviour invites the risk of stress and injury from forced copulation attempts. Male mate guarding tactics are also influenced by the social environment according to male quality and the proportion of neighbouring males not themselves mate guarding and so free to pursue EPCs more actively.

Tests of theory on the costs and benefits driving reproductive strategies

The costs and benefits underlying male reproductive strategies are largely well established with high levels of consensus between different studies (Birkhead 1998). This study offers no real exception to this rule, and confirms the mixed reproductive strategies predictions of sperm competition theory (Birkhead & Møller 1992). It adds a detailed set of behavioural observations of reproductive strategies in a previously unconsidered species, exploring the basis for variation in tactics between individuals and highlighting a rarely considered problem of how individuals may overcome the conflict of competing paternity protection strategies.

The theoretical underpinnings of female reproductive strategies are less well determined than for males, with no clear consensus on the relative costs and benefits or their payoff emerging across species (Birkhead 1998). Here I contribute to the debate both for female extra-pair copulation and for female mate guarding strategies and tactics. Based upon my own data and backed up by a review of the literature, I suggest that the variation in female EPC tactics seen between different species may reflect the counter-strategy by females to avoid the costs of forced copulations in species where males are able to successful sexually harass females. For female mate guarding, I contribute both a new suggestion for a tactic that females may use and, backed up by a review of the literature, suggest that the theory of the costs and benefits underlying female mate guarding needs to be reconsidered to take into account the lack of female mate guarding when the risks of loss of male parental care are low.

Overall Contributions

In this thesis I contribute to our knowledge and understanding of European blackbirds by providing details of how the reproductive strategies of individual birds give rise to the known patterns of breeding biology and ecology in this species.

To the theoretical knowledge in behavioural ecology I add tests of the current theory on the costs and benefits driving sexual behaviour using a detailed set of behavioural observations. In particular I highlight the importance of considering both the ecological and social influences on behaviour and add an exploration of the limits imposed by these factors on mate acquisition and subsequent sexual strategies. I confirm the predictions of sperm competition theory for male sexual strategies and find patterns of behavioural tactics broadly in agreement with other territorial bird species. However, I add knowledge to the rarely considered problem of how individuals overcome the problem of competing paternity protection strategies. As in other bird species, the cost and benefits underlying female

blackbird sexual strategies are less clear, but here I add to the debate with a consideration of how social influences may shape female EPC tactics. I offer an extension of our understanding of female mate guarding by suggesting an alternative tactic that females may use and I point out that the differences in strategies adopted by females in monogamous and in facultatively polygynous species suggest the need for a development of current female mate guarding theory.

To knowledge in avian research I add a detailed set of observations of sexual strategy behaviour in European blackbirds and I suggest a method of colour ringing birds that overcomes the potential problem of influencing behaviour by differences in the colour of rings of individuals.

Implications for Future Work

This thesis has provided an account of the selection pressures shaping the reproductive strategies of urban European blackbirds. Providing the implication of Chapter Two is correct and the data collected here is representative of European blackbirds in general, then the implications are that these selection pressures may have shaped the morphological as well as the behavioural characteristics of the species.

The evidence presented in this thesis suggests that competition for territories containing high quality nesting habitat is more influential on the settlement patterns of female blackbirds than considerations of male quality. As a consequence there is little scope for selection due to female choice of males during mate acquisition. There is, however, considerable scope for selection due to intra-sexual contests for territories in the weeks leading up to pair formation (Snow 1956), and throughout the breeding season.

Once breeding pairs have formed, mixed reproductive strategies by females, with their genetic consequences for paternity of the offspring, provide scope for selection by female choice of intruding males for unforced extra-pair copulations. The responding EPC-seeking strategies by

neighbouring males to take advantage of female mixed strategies, and the countering paternity protection tactics by resident males, provide scope for selection due to male-male competition for paternity. Finally, male-male competition for paternity during group pursuits of fertile females generate further opportunity for selection due to contests between males.

In contrast to these implications for the nature and timing of selection in the Oxford Botanic Garden blackbirds, birds in monogamous reproductive patterns are traditionally expected to be subject to selection due to female choice of males during mate acquisition (Darwin 1871, Fisher 1958, O'Donald 1980, Kirkpatrick et al 1990). More recently, Møller (1992) has argued that further selection may arise through female choice for EPC mates during the breeding season, and predicts that this will enhance the selection due to female choice at mate acquisition. Several studies provide evidence for selection in monogamous species of birds following these expectations (Andersson 1994).

However, Davies (1992) has suggested that mate acquisition due to female settlement on breeding territories primarily in relation to female-female competition and largely independently of male distribution, may be widespread and so apparent lack of selection due to mate choice during mate acquisition may not be confined to the Oxford Botanic Garden blackbirds.

The next step in research into sexual selection in blackbirds must be to investigate the correlations of these selection pressures and the expression of sexually dimorphic characters, to begin to unravel the enigma of such marked plumage and bill dimorphism in this socially monogamous species.

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Appendices

Creighton, E. & Hosie, C. M. 1993a. Beyond mating systems: the need for a new approach. In: *Beyond Mating Systems: collected essays from an ASAB funded workshop* (Col. by: E. Creighton & C. M. Hosie). Milton Keynes: The Open University.

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Beyond Mating Systems

Organised By
Lottie Hosie & Emma Creighton
The Open University

ASAB Funded Workshop
5-6th November 1993
Milton Keynes

Foreword

> *'New approaches are required to expand our understanding of mating patterns, particularly when tackling the greater scope of mating patterns revealed by considering individual variation...'*
>
> Ahnesjö et al 1993. *Behavioural Ecology* 4,187-189.

The above quote resulted directly from an ASAB-funded workshop held in Glasgow in 1991. It reinforced our developing ideas in this area and encouraged us to seek ASAB funding for a workshop to discuss them. Pulling together some of our thoughts on the need for new directions in mating systems research, we wrote an essay to stimulate a response from researchers working on as wide a range of species and from as many different perspectives as we could find. We contacted mainly younger researchers as we felt that opportunites for intensive discussion were limited for people like ourselves, who are at a relatively early stage in their career. Three senior researchers, Nick Davies, Tim Halliday and Phyllis Lee, were also invited to temper enthusiasm with experience. Participants produced their initial essays in response to the first one from us. What follows here are those essays re-written, to a greater or lesser degree, in the light of their experience of the workshop.

Many thanks then, are, due to ASAB for financially enabling us to carry out our plans and also to the Biology Department at the OU for administrative assistance. We all met at the Cock Hotel (of 'Cock and Bull story' fame!) in Stony Stratford, Milton Keynes, on the weekend of 6th and 7th November 1993. Two days of intensive discussion waxed and waned, the wheel was re-invented with a new coat of paint and wobbled home tired but happy! The ideas discussed will feed back into people's thinking and result in subtle but important shifts in perspective when considering mating behaviour. If this eventually leads to new approaches that provide greater insight into animal reproductive behaviour then our aims for the workshop will have been fulfilled

We would like to thank participants, firstly for being keen to attend, secondly, for producing essays promptly and finally, for their enthusiastic participation during the weekend. We enjoyed organising the meeting and meeting everyone, thanks again ASAB.

Lottie Hosie & Emma Creighton,
November 1993, Milton Keynes.

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Beyond Mating Systems: The Need For A New Approach

Emma Creighton & Lottie Hosie

August 1993, Department of Biology, The Open University, Walton Hall, Milton Keynes.

Mating systems have been central to our understanding of animal reproductive behaviour since Emlen & Oring (1977) suggested that the different systems they defined, arose as a consequence of the interaction of general principles. The search for these general principles has continued since.

In a recent review of mating systems, Davies (1991) suggests that these general principles centre around variation in the dispersal of receptive individuals, and the variation in parental care requirements. This generates an authoritative and wide-ranging account of how the various mating systems observed in nature come about. But it is not without its criticisms.

Following Emlen & Oring (1977), the mating system approach attempts to pigeon-hole species or populations into pre-defined categories or systems, depending upon how mates are acquired, their number, the nature of the bond between the sexes, and the parental care provision. The implication is that these four characters vary together across the different species in each system, and that all animals classified within a given system evolved their reproductive behaviour patterns in response to the same selective pressures. However, they are quite separate behavioural patterns. They arise independently from each other in response to different selective pressures: consequentially they vary independently. Any particular combination of the four mating system parameters that superficially look similar in different species, will have arisen as a consequence of convergence, not of co-evolution, as the mating system perspective implies.

Further problems arise when behaviour other than the four characters listed above are considered. For example, many bird species are socially monogamous during the breeding season, yet sexually, extra-pair copulations are widespread (Birkhead & Møller 1992). However, mating system classifications concentrate on the social organisation at the expense of the sexual, even though it is sexual behaviour that is ultimately important in evolutionary terms. Similarly, the temporal organisation of mating behaviour is not a primary consideration. So, for example, monogamy includes animals which pair for life with those which pair with a different partner for each breeding season, without regard to their different evolutionary implications.

Perhaps most significantly, mating systems concentrate on the behaviour of the majority. Minority or mixed reproductive strategies tend to be overlooked or dismissed. Yet these strategies are as much the product of selection as the majority, and if we are to fully understand animal reproductive behaviour they too have to be considered. Associated with this is the bias of the categories towards the sex which does best, so for example, a pattern involving one male and two females is classed as polygynous, emphasising the male's access to multiple partners, even though the two females are sexually monogamous.

The impetus behind this workshop is the question of whether these criticisms are the natural aberrations of any healthy theoretical construct that attempts to explain something as complex and variable as animal reproductive behaviour; or whether they describe a fundamental failing of the mating systems approach to adequately account for this complexity. The workshop will discuss if the mating systems approach is still adequate to direct the exploration of animal mating behaviour, or if it is necessary, and indeed possible, to replace it with something else.

A tall order perhaps? But we would like to suggest that the mating systems approach has already been superseded, and that a new approach exists in a disjointed form. What is needed is a concerted effort to piece it all together, to explore its parameters and to examine their ubiquity across a broad range of taxa.

A closer look at the criticisms sketched above will reveal that they all have the common complaint that mating systems do not account for the observed variation either between individuals across a species or population, or within individuals across time. *Mating systems deal with the common behaviour of members of a group, not the behaviour of individuals themselves. Yet it is the individual, not the group, that is the raw material of evolution. It is the individual who expresses a particular reproductive pattern in response to all the varied selection pressures that act upon it: not the group in response to the common selection pressures acting upon its members.* It is this fundamental flaw, this top-down, group-centred approach to reproductive behaviours that lies at the root of the mating systems problem. The solution, we believe, is to replace it with a new, bottom-up, individual-centred approach.

We have already stated that this shift in emphasis from the group to the individual is not new. Perhaps the best known example is the work of Nick Davies and his colleagues on the dunnocks in Cambridge Botanical Garden

In his book *Dunnock Behaviour and Social Evolution* (1992) Davies describes how, within the constraints of their phylogenetic, ecological and social pre-adaptations to reproduction, the dunnocks adopt sexual strategies that aim to maximise their reproductive success. The outcome of these strategies depend upon the constraints of local habitat, social competition (and perhaps life experience), that act upon each individual, and result in a whole array of different reproductive patterns within the population.

The point is that the dunnock reproductive patterns arise as a consequence of individual-specific constraints acting upon the individuals, not as a consequence of the interaction of general principles common to all animals exhibiting those particular mating systems. In accounting for the variation in dunnock reproductive patterns, Davies and his team have in fact made the shift from the top-down, group-centred, to the bottom-up, individual-centred approach. The Cambridge dunnock variations are not mating systems in the classic sense, they are individual reproductive patterns.

So, if this shift in thinking has begun, why the workshop? Well, it seems that we have arrived at the unusual position in Behavioural Ecology where the practice is ahead of the theory. Field studies are being interpreted in terms of individual reproductive strategies, but the theory appearing in the reviews is still group-centred. We have yet to formally recognise this shift in thinking and to develop it into a new theory to guide future research. By gathering together 21 people actively involved in the practice we aim to start the process.

Your brief is to examine your own approaches to interpreting behaviour observed in the field, and to identify and describe the constructs used in that interpretation. Examine the details of the variations in behaviour which are shown by individuals, with the aim of identifying the constraints and/or determinants that influence the expression of their reproductive pattern. Participants have been invited from as wide a range of backgrounds as we could find, so each approach will be different, but should contain common themes that can be built into a general theoretical framework.

There are two main areas to think about. Firstly we need to consider the *potential* reproductive patterns (or spectrum of patterns) that any individual might be predisposed to employ in a particular breeding season or attempt. This involves identifying key areas where selection might have operated in the past, and how they might have combined to 'produce' (evolutionarily) the potential reproductive patterns available to an individual.

The second area to consider is not what may have happened in the past,

but for any particular breeding event, what immediate constraints direct the *actual* reproductive pattern (of the spectrum of potentials) an individual employs.

We have deliberately not explained in too much detail how this approach might be used for any individual species, as we want you to consider it using your own experiences with your particular animals. At this stage we feel that what is most important is to do some serious wide-ranging thinking!

This communication is intended as a stimulus to participants to start the process off. You are each invited to communicate your thoughts through an essay of approximately 1000 words which will be circulated to all participants prior to the workshop. Include comments on your own approaches to the problem, identify the constructs you have used, and speculate on their ubiquity to a general approach for understanding animal reproductive behaviour. Let your imagination go into over-drive, be controversial, provocative, outrageous even! It is intended that these essays are unconstrained by the literature or convention. You will not be asked to rigourously defend your ideas, but to elaborate upon them: they are to act as a stimulus for discussion. You will have the chance to rewrite them into a more conventional format for wider circulation after the workshop.

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Beyond Mating Systems: A suggestion For A New Approach

Emma Creighton & Lottie Hosie

November 1993, Department of Biology, The Open University, Walton Hall, Milton Keynes.

It is easy to criticise a body of knowledge, to pick holes in its structure and point out its short comings. The difficult part is in suggesting an alternative. Our first communication did the criticising, this one is a tentative attempt at suggesting an alternative. In it we offer a new framework for looking at animal reproductive behaviour, one based upon individuals, and one which we hope will evolve to be more effective as a starting point for understanding animal reproductive behaviour than the conventional mating systems approach.

Our thesis is that the observed patterns in animal reproductive behaviour arise out of the interaction of the reproductive strategies adopted by individuals meeting to reproduce. These strategies are varied within individuals and different between them, and depend upon the interaction of a multitude of features which influence an individual's attempts to maximise its reproductive success. In order to account for observed animal reproductive behaviour, these factors must be identified and defined, and their effects on individuals studied to see if there are any common themes which arise and are applicable to animals across the taxa. We propose the "Any Port in a Storm" analogy to predict how they might interact (see below), but as a starting point we argue that they can be grouped into ecological, social, life history and life-experience influences, and that these fall into two distinct groups of influence: those which have constrained the evolution of an animal's *potential* reproductive strategies, and the more immediate ones which influence which *actual* strategy is expressed.

Constraints on Individual Reproductive Strategies

Figure one overleaf summarises the grouping of the factors which constrain individual reproductive strategies. To expand the idea, a given animal is not totally free to adopt any reproductive strategy imaginable. It is restricted into a narrow band of strategies by its evolutionary past, which has shaped its anatomical, physiological and to a large extent, behavioural predispositions for reproduction. Subsequently the animal is limited to potential strategies which are compatible with this genetic pre-disposition. To labour the point, a mammal cannot adopt for external fertilization in water with no parental care, because it is genetically restricted to internal

fertilization, placental growth and extended parental care in the form of milk produced from specialised glands.

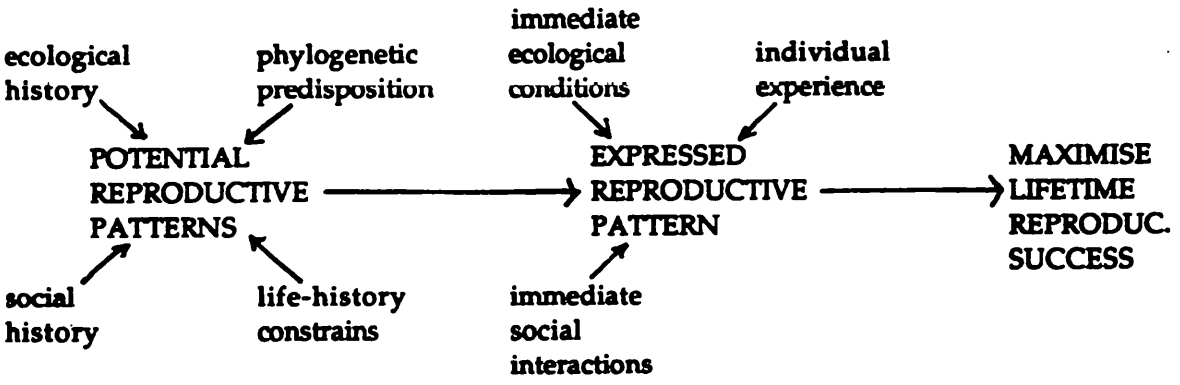

Figure 1. Schematic summary of the constraints influencing an individual's attempts to maximise its lifetime reproductive success.

Any consistent constraints that have acted upon the reproductive success of an animal's ancestors will have exerted selective pressures such that the modern animal will have evolved reproductive behaviour which minimises these constraints. The greater the selective pressure exerted, the more invariable the evolved response will be, and the fewer the potential reproductive strategies the animal will be free to employ. So, for example, individuals of a species adapted to harsh environments are likely to be restricted to similar reproductive strategies, which will generate similar reproductive patterns throughout; whereas those adapted to breeding in more forgiving habitats, are likely to display a range of strategies and subsequent reproductive patterns.

"Any Port in a Storm" Analogy

Animals that have inherited the potential for expressing a range of reproductive strategies are faced each breeding cycle with the decision of which to adopt. We argue that the decision will be made in response to the restrictions on reproductive success that each individual animal finds itself under at that particular time, and the strategy adopted will be that which, by its expression, aims to maximise the individual's lifetime reproductive success within those restrictions. Specifically, the resource which is in the shortest supply will be the most limiting, and we predict that each individual will give priority to securing this resource before all others. Only then will it turn its attention to its other needs, and again these will be prioritised according to their limiting effect.

Discussions of this approach with Jamie Dick at the workshop generated

the analogy with a ship caught in a storm. For the ship, the most limiting resource is shelter, and it should head for the nearest port regardless of its requirements once in port. Only when shelter is secured can the sailors turn their attention towards maximising the supplies they need which will be limited by those available in that particular port.

This analogy neatly illustrates the fact that an animal may have to make do with less-than-optimal resources due to the limitations imposed by its need to secure a most limiting resource. So, for example, female blackbirds face very high nest predation, and the most limiting resource on their reproductive success is nest cover. To limit this restriction, females compete with each other for territories containing good cover, and then accept as a territorial mate the male overlapping this territory (Creighton in prep.). This mate may not be of the highest quality, but the parental care he provides raises her reproductive success, and she may be able to secure extra-pair copulations with higher genetic quality males.

The nature of the limiting resources for other animals will depend upon their inherited requirements and the environment in which they find themselves. In practice these may be difficult to discern, but should be a major aim of fieldwork to identify the nature of both the factors which have determined the spectrum of potential reproductive patterns, and those which dictate the actual strategy expressed. Obviously they will differ between each species, otherwise we would have no variation in reproductive behaviour whatsoever! but we believe they can be identified, and indeed have been discussed in the mating systems literature. Most notably they will differ between the sexes within a species, as their reproductive requirements differ, and they will depend upon the specific ecology of the habitat. They may vary spatially between habitats, and temporally over a season and between years. We believe that it is this variation that accounts for the differences in reproductive behaviour that are observed between individuals of a species, and that these differences in individual behaviour contribute to the differences in the gross reproductive patterns between different populations within a species, and indeed between the gross reproductive patterns of species themselves.

What is lacking is a concerted attempt to pull it all together into a logical, individual-centred framework, and an exploration of how they interact to predict/account for the observed variation in animal reproductive patterns. It is hoped that this can be achieved by computer simulation, and future work in this direction is planned.

Individual Reproductive Strategies and Reproductive Patterns

Throughout this essay, we have refered to the term *reproductive pattern* to describe the outcome of *individual reproductive strategies*. Ironically, one of our contentions with the mating systems approach is the minefield of terminology it generates, yet we feel the need to add these two terms to emphasise the difference between the conventional and the new individual-centred approaches.

The need for an over-all description of the patterns of animal reproductive behaviour is important, and is illustrated by the contribution mating systems classifications have made to our understanding. It is intuitive that there is a pattern to the variation we observe, and this should be reflected in the terminology we use. However, we argue that the mating systems approach has major flaws, and that new developments are needed to reflect changes in our understanding and interpretation of animal reproductive behaviour.

Emlen & Oring (1977) recognised that reproductive behaviour is described by four key features, which may be summarised as:

- a description of how mates are acquired,
- the social relationship between individuals coming together to reproduce,
- the pattern of gamete transfer,
- the parental care pattern.

Unfortunately the mating systems approach erroneously assumed these features are related and vary together (Creighton & Hosie this volume). It was recognised by the workshop that these features are in fact quite separate, and vary independently from each other. Consequently the aim of the mating systems approach to pigeon-hole reproductive behaviour into categories, defined by unvarying combinations of these features, is doomed to failure. It was proposed that a phrase summarising the expression of each of these features would be a useful extension of loosely defined umbrella categories. So, for example, "monogamy" applied to European blackbirds, would be expanded by the phrase "seasonal, opportune territorial pairs, with female choice for extra-pair copulations, biparental care" (Creighton in prep). Not only is this a more illuminating description of blackbird behaviour, but the use of such terminology to describe all animal reproductive behaviour would greatly extend the power of comparative approaches in separating out the phylogenetic components of animal reproductive behaviour (see Owens this volume).

Such a phrase we propose is a description of a *reproductive pattern*, not a mating system. The distinction is important. Firstly it emphasises the change in thinking from fitting animals into pre-defined categories, towards accepting the importance of variation in behaviour. Secondly, the word *system* implies a common underlying process, suggesting that all animals exhibiting a superficially similar system do so by the same mechanism. Following the main thesis of this essay, superficially similar reproductive patterns may arise by different processes, by convergence not co-evolution, and we assert that the word *pattern* has fewer implications about the processes generating them. Thirdly, the features which describe animal reproductive behaviour include much more than mere mating, so the word *reproduction* is used to emphasise their inclusion.

The use of the term *individual reproductive strategy* is used to emphasise the separation of the processes of reproductive behaviour from the patterns they produce. It emphasises the individual's role, and that this behaviour is a dynamic process, a strategy, shaped by the animal's environment acting upon its inherited potential.

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Mate Guarding Versus Territorial Defence in the Common Blackbird

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Male Common Blackbirds *Turdus merula* (hereon: Blackbirds) are readily observed escorting their mate as she collects nest material and builds her nest, though courtship and copulations are rarely observed (Snow 1958a). So it is likely that in common with the majority of solitary, territorial passerines (Birkhead & Møller 1992a, Birkhead 1998), male Blackbirds adopt mate guarding by close association as their primary paternity protection tactic (Beecher & Beecher 1979, Birkhead 1979).

However, mate guarding is costly in both time and energy and may conflict with other behaviour (Møller 1987a, Lamprecht 1989, Davies 1992, Westneat 1994). In particular, Blackbirds are strongly territorial and invest heavily in maintaining their territory with high levels of vigilance, patrols of their territory boundaries and by ousting any male who crosses the territory boundary (Snow 1956, 1958a).

Here I report on how male Blackbirds in the Oxford Botanic Garden, UK, resolve these two potentially conflicting demands of mate guarding and territorial defence. I report on how their tactics vary with age and I explore how their behaviour serves to protect their paternity.

DNA finger-printing analyses reveal that extra-pair paternity occurs in this population (14% of chicks (2/14) in 29% of broods (2/7), Creighton 2000). Observations of behaviour suggest that paternity is lost when females occasionally accept the courtship advances of intruding males (Creighton 2000) and possibly when several males intrude onto the territory simultaneously to chase the female and force copulations upon her (Creighton 2000, but see Gowaty & Buschhaus 1998).

The mate guarding hypothesis predicts that males should remain in close association with their mate during her fertile periods (Birkhead & Møller 1992a, Birkhead 1998). However, territorial defence as a paternity protection tactic to prevent other males from gaining sexual access to the female (Møller 1987b, 1990) also predicts that males should engage in higher levels of territorial defence during the females' fertile periods. Since males have to leave their mate to patrol their territory boundaries and to oust intruding males, these two paternity protection tactics appear to be in direct conflict with each other.

Methods

I observed the Blackbirds in Oxford Botanic Garden (51°44'N,1°16'W), Oxfordshire, UK, from February to mid-June 1991-93. The birds were caught yearly in Potter traps (Davis 1981), were colour ringed and were aged and sexed by plumage characteristics (Snow 1958a). Sixteen different male-female pairings, involving 12 males and 13 females, were followed over 41 nesting attempts (37% first attempts, 39% second, 22% third and 2% fourth attempts). Focal pairs were observed for up to 20 minutes per day across all stages of their attempts, usually between 0600 and 1100 BST (mean watch duration was 18.3 min., averaging 5.5 watches per attempt, with a total observation time of 67.4 hours). At one minute intervals estimates were made of 1) intra-pair distance in metres, 2) whether the pair members were in visual contact, and 3) the height in metres above ground of each focal bird. When a bird was out of visual contact with its mate (eg over a wall or on the other side of the territory) a distance of >25 m was recorded. Further behaviour was recorded as it occurred. 4) Initiation of moves of a distance greater than 5m or out of perceived visual contact with the mate, and whether the mate followed within 30 secs. 5) Rendezvous moves to within 10 m and perceived visual contact of the mate, made after the pair had been separated for longer than 1 min. and/or had been involved in independent

activities. 6) Duration of boundary patrols by the male. These included display flights between vantage points around the periphery of the territory and trips to oust intruders or to engage in boundary disputes with neighbours. 7) Territory boundary displays (Snow 1958a) or fights.

The data were organized into four stages of the females' reproductive cycle, where day zero indicates the day the first egg was laid. *Pre-fert:* days up to and including the sixth day (day -6) before the first egg was laid. This is prior to the earliest day that copulations have been recorded in Blackbirds (after pair formation is complete) (Snow 1958a, pers obs). For first attempts data collection began after pair formation (Snow 1958a), for replacement attempts it began the day after the previous attempt was lost, and for second broods it began 11 days before the initiation of the next clutch.

Fert: between 5 and 2 days before the first egg was laid (days -5 to -2). This was prior to ovulation and fertilization (see below), but included the period in which copulations have been recorded in Blackbirds (Snow 1958a, pers obs). Given that the shortest known duration of sperm storage in birds is 6 days (Birkhead & Møller 1992b), sperm inseminated during copulations in this period could fertilize eggs during laying.

Egg-fert: from the day before the first egg was laid until the day the penultimate egg of the clutch was laid. Given that fertilization occurs 24 hours before each egg is laid (reviewed in Birkhead 1998), the female was fertile on these days.

Inc & brood: including the day the last egg was laid, 13 days of incubation and 13 days of brooding (Snow 1958a, 1958b).

Rates of behaviour per minute were derived from the duration of the watch and when combining data from several watches, averages were weighted by watch duration.

Results

Intra-pair distance varied over the stages of the females' reproductive cycle (Table 1), decreasing to a minimum during the *Fert* and *Eggfert* stages, after which it increased. This decrease in intra-pair distance was associated with the peak in the proportion of female-initiated moves followed by the male, but not with any changes in the proportion of male-initiated moves followed by the female (Table 1). The proportion of moves made by the male which brought the pair members together, and the proportion of time the pair spent in visual contact did not vary with the stages of the female's reproductive cycle (Table 1).

Following Davies and Hatchwell (1992) and Hatchwell and Davies (1992), these analyses assumed that data collected from each breeding attempt were independent, although six pairs contributed only one attempt, ten contributed two or more (range 2 to 7, median 2.4). However, the variation in the intensity of paternity assurance measures between these pairs was no greater than that exhibited by the individual pairs over repeated attempts, indicating that the data were not biased by these repeated measures (1-way ANOVA: intra-pair distance after $\log_{10}$ transformation, $F_{9,34}=1.19$, $P=0.347$; male follows female after arcsine transformation, $F_{9,34}=1.47$, $P=0.212$).

A second potential source of error arises from treating each unique male and female combination as statistically independent even though some birds were included twice when with different partners in different years. However, conservative analyses of the paternity assurance measures

using data from each individual in only one pairing (after Davies & Hatchwell 1992) show similar results as the full analyses and indicate that the data were not biased by repeated measures (Friedman two-way ANOVA: intra-pair distance, Fr_3=27.81, P<0.001; male follows female, Fr_3=10.07, P=0.018; female follows male, Fr_3=0.171, P=0.982; male rendezvous, Fr_3=2.97, P=0.396, visual contact Fr_3=1.64, P=0.649).

Males did not normally associate with their mate on the ground, but typically perched above her (mean +se) perch heights in meters across all stages of the females' cycle: males 2.30 +1.04; females 0.67 +0.61; Wilcoxon Signed Ranks Test, Z_{16}=3.46, P<0.001).

There was no variation over the stages of the females' reproductive cycle in either male perch height, in the proportion of time males spent patrolling their territory boundaries nor in the rate at which they engaged in boundary disputes (Table 1).

First-year males remained closer to their mates over the *Fert* and *Eggfert* stages of their mate's cycles than did older males. There was a tendency for first-year males to follow more of their mates' moves than older males, but this was not statistically significant (Table 2). However with only three first-year males breeding on the site, the power of this statistical test is low (>80% chance of a type II error).

Low statistical power may also account for the lack of statistical differences in territorial behaviour with male age. However, from the data available (Table 2) there is little suggestion of any real differences. For all three measures the degree of overlap of the scores, as indicated by the inter-quaternile range (IQR), is much larger than any differences between the medians.

Discussion

Male Blackbirds remained closer to their mate and followed more of her moves in the days leading up to and during egg laying. This corresponds to the females' presumed fertile period and is consistent with the mate guarding hypothesis (Birkhead & Møller 1992a, Birkhead 1998).

Male perch height, amount of time spent patrolling his territory and engagement in boundary disputes remained constant across the stages of the females' reproductive cycle, and indicated that males maintained an equal intensity of territorial defence independently of female fertility. This contradicts the hypothesis that territorial defence functions explicitly as a paternity protection tactic, but rather suggests that territorial defence serves functions that persist throughout the females' cycle.

The pattern of male mate guarding was somewhat dissimilar to that typically found in other passerine species, as males did not remain on the ground within the "safe" 5m mate guarding distance of their mate (Davies 1985, Alatalo *et al.* 1987, Møller 1987c, Birkhead & Møller 1992a). Rather males habitually perched in a prominent position above their female, gaining good views of their mate and of much of their territory. A similar pattern of behaviour is found in Yellowhammers *Emberiza citrinella,* in Yellow Warblers *Dendroica petechina* and in Red-faced Warblers *Cardellina rubifrons* occupying open habitat with good visibility (Hobson & Sealy 1989, Sunberg 1992, 1994, Barber *et al* 1998), and may be a modification of mate guarding behaviour afforded in open habitat that permits both scrutiny of the female's behaviour and monitoring of the territory for intruders.

The maintenance of intra-pair distance by male but not female Blackbirds may reflect a conflict of interest between the sexes over mate-

guarding (Lifjeld *et al.* 1994). Indeed females show apparent attempts to avoid their mate's mate guarding attentions by initiating more moves away from him during their presumed fertile periods (Creighton 2000), and will occasionally accept the courtship advances of extra-pair males who succeed in approaching the female without being detected by the resident male (Creighton 2000). By remaining close to the female, males can prevent extra-pair copulations and so protect their paternity by thwarting the female's extra-pair copulatory strategies.

It might appear that territorial defence occurs in direct conflict to mate guarding behaviour since the male must leave the female to patrol the territory, to oust intruders and to engage in boundary displays with neighbours. Yet it continues during the fertile stages of the females' reproductive cycle. However, by preventing the access of other males to the territory, it serves to limit their access to the female and so may act as a secondary paternity guard.

The maintenance of territorial behaviour over the whole of the female's cycle suggests that it serves additional functions to paternity protection. High perch heights may aid predator detection or allow the male to observe other females on neighbouring territories and so aid the male's own extra-pair copulatory activities (Hobson & Sealy 1989). The maintenance of territorial boundaries may reflect the unpredictable re-mating opportunities afforded by the high rate of nest predation in Blackbirds (50-95%, Snow 1955, 1958a, Osborne & Osborne 1980, Desrochers 1991, Groom 1993, Hatchwell *et al* 1996) and ensures that the male has a viable territory whenever his mate becomes fertile.

The intensity of mate guarding was greater in first-year males than in older, but there were no differences with male age in the intensity of

territorial defence. This may reflect greater mate guarding efficiency in older birds due to their greater experience; but if this was the case, older males did not trade lower mate guarding intensity for greater territorial defence. Alternatively it may reflect differences in quality, if age reflects quality due to longevity (Manning 1985, Hansen & Price 1995, Kokko 1997, Møller & Ninni 1998) and lower quality males guard more intensely as a "best of a bad job" strategy (Trivers 1972, Dawkins 1976) when females seek extra-pair copulations with higher quality males (Gowaty & bridges 1991, Kempenaers *et al* 1992, 1995, Lifjeld *et al* 1994, Johnson & Lifjeld 1995, Wagner *et al* 1996). Since male mate guarding in this study appears to function to prevent females engaging in extra-pair copulations, and females on this study site were found to move away from their guarding mates so creating opportunies for extra-pair copulations (Creighton 2000), it is likely that younger males guarded more intensely as a reflection of their higher risk of losing paternity due to female choice. Older, higher quality males with a lower risk of loss of paternity guarded less, perhaps trading lower intensity guarding for greater extra-pair copulation effort (Creighton 2000).

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Table 1. Summary of the changes in male mate guarding behaviour and male territorial defense behaviour over the stages of the females' reproductive cycle. Data are presented as medians (+IQR) or [range] for N attempts. Friedman two-way ANOVA results are for 27 breeding attempts with data available for all four stages

	Pre-fert	Fert	Egg-fert	Inc & brood	*Fr*	*P*
Mate Guarding						
Intra-pair distance (m)	14.60 (7.89)	8.56 (5.00)	9.67 (7.85)	17.00 (4.95)	34.97	0.000
Male follows female	0.12 (0.31)	0.57 (1.00)	0.30 (0.67)	0.00 (0.00)	13.67	0.003
Female follows male	0.00 [0.00]	0.00 [0.39]	0.00 [0.50]	0.00 [0.20]	0.13	0.988
Male rendezvous	0.21 (0.67)	0.63 (1.0)	0.20 (0.55)	0.25 (0.52)	2.78	0.427
Visual contact	0.95 (0.24)	0.94 (0.15)	0.92 (0.19)	1.00 (0.17)	2.17	0.539
Territorial Defence						
Male perch height (m)	1.25 (1.19)	2.80 (2.54)	2.45 (3.45)	2.20 (3.35)	2.66	0.448
Proportion time patrolling	0.03 (0.13)	0.05 (0.15)	0.09 (0.19)	0.00 (0.12)	2.17	0.539
Rate boundary disputes (hr^{-1})	0.00 (0.03)	0.00 (0.05)	0.00 (0.05)	0.00 (0.03)	2.99	0.393
N	39	39	32	27	df = 3	

For inter-pair distances, the differences lie between the Prefert and Fert stages, and the Eggfert and Inc & Brood stages, at α=0.05. For the proportion of female moves followed by the male, the difference lies between the Prefert and Fert stages, at α=0.05.

Table 2. Summary of the differences in male mate guarding behaviour and male territorial defense behaviour between first year and older birds. Data are presented as medians (+IQR) over the Fert and Egg-fert stages for all attempts by each individual in each year. Statistics are Mann-Whitney U tests

	1st yr male	Older male[1]	*U*	*P*
Mate Guarding[2]				
Intra-pair distance (m)	7.83 (5.59)	9.40 (3.82)	6.0	0.035
Male follows female	0.75 (0.38)	0.48 (0.52)	9.0	0.069
Territorial Defence				
Male perch height (m)	1.43 (2.18)	2.47 (2.45)	21.0	0.547
Proportion time patrolling	0.15 (0.11)	0.12 (0.15)	23.5	0.724
Rate boundary disputes (min^{-1})	0.01 (0.02)	0.01 (0.03)	22.5	0.642
N	3	18		

1. No first year males were later included as older males,

2. Differences were not due to the age of female in the pair.